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PAR
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LE RÔLE DES CROÛTES BIOLOGIQUES DANS LA SUCCESSION DES PLANTES VASCULAIRES SUR UN TERRAIN PROGLACIAIRE DANS LE HAUT-ARCTIQUE CANADIEN

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AVANT-PROPOS

Ce mémoire de maîtrise est l'accomplissement de mes recherches effectuées sous la direction de la professeure Esther Lévesque. Il comprend trois chapitres, dont deux sont sous forme d'article scientifique et sont rédigés en anglais. Par conséquent, certaines répétitions surviennent dans la description du site d'étude et dans la méthodologie de recherche utilisée. Le mémoire inclut un résumé en français (Chapitre 1) dans lequel sont exposés la problématique, les objectifs, la méthodologie, les résultats et les conclusions.

Les deux articles sont basés sur mon travail de terrain durant l'été 2004 devant le glacier « Teardrop » à Sverdrup Pass, Île d'Ellesmere, Nunavut dans l'Arctique canadien. Le premier article (Chapitre 2) : « *Proglacial succession of biological soil crusts and vascular plants: biotic interactions in the High Arctic* » fournit de nouvelles connaissances sur les croûtes biologiques et leurs interactions avec les plantes vasculaires durant la succession végétale. Le deuxième article (Chapitre 3) : « *The influence of biological soil crusts on soil characteristics along a high arctic glacier foreland, Nunavut, Canada* » caractérise le développement des sols le long d'un terrain proglaciaire. Il souligne le rôle joué par les croûtes organiques dans l'amélioration des conditions édaphiques. Les informations complémentaires qui n'ont pu être incluses dans les articles scientifiques se trouvent en annexe du mémoire.

Les deux articles scientifiques seront soumis pour publication dans des revues à comité de lecture. Je suis première auteure de ces articles et ma directrice, Esther Lévesque, en est co-auteure.

REMERCIEMENTS

Premièrement, j'aimerais remercier et souligner l'implication des membres de mon comité : Esther Lévesque, Alain Maire et Guy Samson. Ils ont manifesté de l'intérêt pour mon projet, m'ont porté assistance et ont nourri ma réflexion de leurs commentaires. Merci particulièrement à ma directrice de recherche, Esther Lévesque pour son enthousiasme, son énergie et ses encouragements sans fin envers moi et mon projet. Ce fut un grand plaisir que de travailler et d'apprendre avec elle, j'ai pu ainsi approfondir mes connaissances et opinions sur la science, l'Arctique et l'environnement.

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RÉSUMÉ SUBSTANTIEL

1.1 INTRODUCTION

Depuis la fin du Petit Âge Glaciaire (PÂG; environ 1850), le réchauffement global a provoqué une réduction des superficies englacées dans le Haut-Arctique canadien (Dowdeswell, 1995). La colonisation des terrains récemment exposés par des microorganismes et des plantes vasculaires, crée un gradient environnemental ayant une complexité écologique croissante en s'éloignant du front du glacier. La dispersion, la colonisation et le développement des organismes microbiens et des plantes vasculaires le long d'un terrain proglaciaire sont limités par plusieurs facteurs. Ces barrières peuvent être dues aux différents mécanismes de dispersion, au manque de propagules, aux sols peu développés, au manque d'éléments nutritifs, à la variabilité de la disponibilité en eau et aux températures froides (Billings, 1987). La plupart des terrains proglaciaires sont constitués principalement de dépôts glaciaires et fluvio-glaciaires et, par endroits, de sédiments ou de sols fins où poussent des plantes isolées dotées d'un fort potentiel de recrutement, ainsi que d'une biomasse, d'une diversité et d'une productivité faibles (Peet, 1992).

La colonisation primaire et la succession primaire des environnements stériles doivent d'abord être considérées comme étant de nature microbienne (Hodkinson *et al.*, 2002). Effectivement, les microorganismes pionniers, tels que les cyanobactéries, les algues vertes et autres bactéries hétérotrophes, sont les premiers à coloniser la surface et la sous-surface des sols dénudés. Par la suite, viennent les lichens, les mousses et les champignons microscopiques. Après un certain temps, un groupement de ces organismes peut engendrer une couche organique vivante à la surface du sol, nommée 'croûte biologique' (Evans et Johansen, 1999; Belnap et Lange, 2001). Les premiers inoculants microbiens de la communauté sont les précurseurs de l'éventuel développement de la croûte (Wynn-Williams, 1993). Ils jouent un rôle crucial en créant la base d'un milieu organique riche en nutriments dans lequel les organismes plus complexes vont s'établir (Smith, 1991). Compte tenu de leurs particularités intrinsèques, les terrains proglaciaires de l'Arctique représentent donc des terrains privilégiés pour l'étude de la colonisation, de la succession et des interactions biotiques entre les croûtes biologiques et les plantes vasculaires.

Les régions les plus arides au Canada comportant des croûtes biologiques sont les déserts et les semi-déserts polaires du Haut-Arctique, qui représentent 95% des territoires libres de glace de ces hautes latitudes (Bliss *et al.*, 1973). Le Haut-Arctique est considéré comme un environnement extrême en raison des basses températures, de la courte saison de croissance et des sols pauvres en nutriments. Ces facteurs entraînent une productivité faible et un recouvrement végétal limité (Billings, 1987; Edlund et Alt, 1989). La plupart des déserts polaires ont une faible diversité de plantes vasculaires et le recouvrement des plantes vasculaires et des cryptogames représentent respectivement 1 à 3 % et 0 à 5 %. Toutefois, certains paysages peuvent avoir un recouvrement pouvant

atteindre 8 à 12 % de plantes vasculaires et 50 à 80 % de cryptogames (Bliss et Gold, 1999).

Des recherches ont montré que la colonisation par des plantes vasculaires est facilitée par le développement préalable des croûtes biologiques (Gold et Bliss, 1995; Gold, 1998; Bliss et Gold, 1999), mais, cette hypothèse n'a pas encore été vérifiée sur un terrain proglaciaire dans le Haut-Arctique. Or, les terrains proglaciaires, avec leur chronoséquence et leur fort gradient environnemental, représentent des environnements privilégiés pour évaluer l'importance des interactions biotiques dans des conditions abiotiques stressantes. Le long d'un terrain proglaciaire, les interactions biotiques interspécifiques et les changements environnementaux peuvent éventuellement engendrer des conditions favorables à l'implantation de nouvelles espèces (Glenn-Lewis *et al.*, 1992).

Plusieurs études ont montré une corrélation positive entre la présence des premières espèces de plantes colonisatrices et fixatrices d'azote et la densité ou la croissance des espèces successives (Lawrence *et al.*, 1967; Blundon *et al.*, 1993; Chapin *et al.*, 1994). Les caractéristiques des croûtes biologiques impliquent qu'elles peuvent faciliter la colonisation, la croissance et le maintien des plantes vasculaires. Effectivement, en enrichissant le sol par l'apport de nutriments et en augmentant les concentrations de divers éléments essentiels pour les tissus des plantes, les organismes qui composent les croûtes biologiques jouent un rôle clé dans le développement des écosystèmes arides (Harper et Pendleton, 1993; Belnap *et al.*, 1997; Harper et Belnap, 2001). Par exemple, dans les régions du Haut-Arctique, l'azote, qui est un des facteurs les plus important pour la croissance des plantes (Henry *et al.*, 1986), est essentiellement fixé par les cyanobactéries du genre *Nostoc* (Archibold, 1995), une composante majeure des croûtes biologiques.

Les croûtes jouent aussi un rôle physique essentiel en stabilisant les surfaces mobiles et en protégeant le sol contre l'érosion (Evans et Johansen, 1999). Dans les régions froides et notamment dans l'Arctique, les mouvements du sol dus aux processus périglaciaires peuvent représenter une source substantielle de stress pouvant même entraîner la mortalité des plantes (Wynn-Williams, 1993; Bliss et Gold, 1994; Gold et Bliss, 1995). Les croûtes contribuent à la réduction de l'érosion par l'eau et par le vent en raison de leur humidité et de leur adhésion, notamment grâce aux gaines gélatineuses des cyanobactéries. De plus, la couleur foncée et la rugosité des croûtes réduit l'albédo et favorise l'augmentation de la température à la surface du sol (Gold, 1998). Le développement des croûtes entraîne ainsi une série de changements physiques, chimiques et biologiques du milieu. Les répercussions des caractéristiques des croûtes seront quantifiées et discutées dans les deux chapitres suivants.

1.2 PROBLÉMATIQUE

Les processus qui surviennent dans le sol suite à la déglaciation et le rôle écologique joué par les croûtes biologiques dans leur relation avec les plantes vasculaires sont peu connus. Une étude approfondie du développement des croûtes biologiques est essentielle afin de connaître leur capacité à favoriser et soutenir la colonisation par les plantes

vasculaires. Les microbes présents dans les croûtes biologiques peuvent coloniser une variété d'habitats extrêmes (Belnap et Lange, 2001). De plus, la colonisation et le maintien des plantes dans le Haut-Arctique relève plutôt de la présence de microsites ayant des températures du sol ainsi que des teneurs en eau et en nitrates plus élevées (Sohlberg et Bliss, 1984), soit des conditions semblables à celles créées par les croûtes biologiques. Dans ce contexte, je propose l'hypothèse générale selon laquelle l'augmentation en abondance des croûtes biologiques le long d'un terrain proglaciaire crée des microsites ayant des propriétés physiques, chimiques et biologiques favorisant la colonisation et la croissance des plantes vasculaires.

Les hypothèses spécifiques des chapitres 2 et 3 sont respectivement : Chapitre 2) Le développement d'une croûte biologique augmentera le recouvrement, la richesse spécifique et la densité totale et reproductive des plantes vasculaires le long d'une chronoséquence. Chapitre 3) Les conditions environnementales favorables à la croissance des plantes vasculaires seront meilleures en association avec la croûte et elles deviendront de plus en plus favorables en s'éloignant du glacier en raison du développement de la croûte biologique.

1.3 OBJECTIFS

L'objectif général de cette étude est d'évaluer les facteurs favorisant la colonisation des plantes vasculaires le long d'un terrain proglaciaire. L'emphase est mise sur les changements et interactions biotiques et environnementales, le développement des croûtes biologiques et la communauté végétale. La méthodologie combine les mesures biologiques, physiques et chimiques et l'analyse statistique des tendances.

Le chapitre 2 cherche à quantifier la distribution spatiale et le pourcentage de recouvrement des croûtes biologiques le long d'une chronoséquence proglaciaire afin de comparer l'abondance des croûtes avec divers paramètres de succès végétal tel que le recouvrement, la densité, la composition, la richesse spécifique, et le statut reproducteur des plantes vasculaires. En outre, des analyses statistiques multivariées ont été employées afin de déterminer la variabilité dans le recouvrement végétal en fonction de différentes variables environnementales. Le chapitre 3 examine les changements de propriétés édaphiques (notamment la température, le potentiel hydrique, le contenu en eau, la matière organique, la granulométrie, le pH, l'azote total, le phosphore disponible et le potassium échangeable) à l'intérieur et hors du substrat encroûté en relation avec la distance du glacier. L'objectif étant d'évaluer comment ces propriétés influencent les facteurs biotiques mesurés dans le chapitre 2. Dans ces deux chapitres, nos données sont comparées à d'autres terrains proglaciaires dans le monde circumpolaire.

Plusieurs expériences sur le terrain et en laboratoire ont permis d'évaluer l'hypothèse selon laquelle les substrats encroûtés favorisent davantage la rétention et la germination des graines que les sols nus. Des mesures détaillées de retrait du front glaciaire et du diamètre des plantes et des lichens en fonction de la distance au glacier ont aussi été réalisées. Ces données sont présentées en annexe.

1.4 MÉTHODOLOGIE

La recherche a eu lieu sur le terrain proglaciaire du glacier Teardrop sur l'Île d'Ellesmere, Nunavut (79°10'N, 79°45'W) du 26 juin au 11 août 2004. L'Île d'Ellesmere fait partie de la zone de végétation polaire désertique (Edlund et Alt, 1989). La région reçoit moins de 150 millimètres de précipitations par année et la température atmosphérique moyenne de juillet varie entre 3 et 5 °C (Maxwell, 1981). Le terrain proglaciaire du glacier Teardrop est situé près de la ligne de partage des eaux du Col Sverdrup (« Sverdrup Pass »), une vallée divisant le centre de l'Île d'Ellesmere d'est en ouest (Figure 1.1). Le maximum glaciaire atteint au Petit Âge Glaciaire (environ 1850) marque la limite du terrain récemment déglacé. Cette limite est tracée par une moraine terminale de même qu'une zone de mortalité de lichens. Des comparaisons entre des photos aériennes prises en 1959 (Photothèque National de l'Air, Ottawa) et des mesures *in situ* ont permis à Fahselt *et al.* (1988) de déterminer le taux annuel de recul du front glaciaire entre 1959 et 1986. Nos mesures prises au cours de l'été 2004 complètent leurs travaux et permettent de documenter les changements récents de la position du front glaciaire.

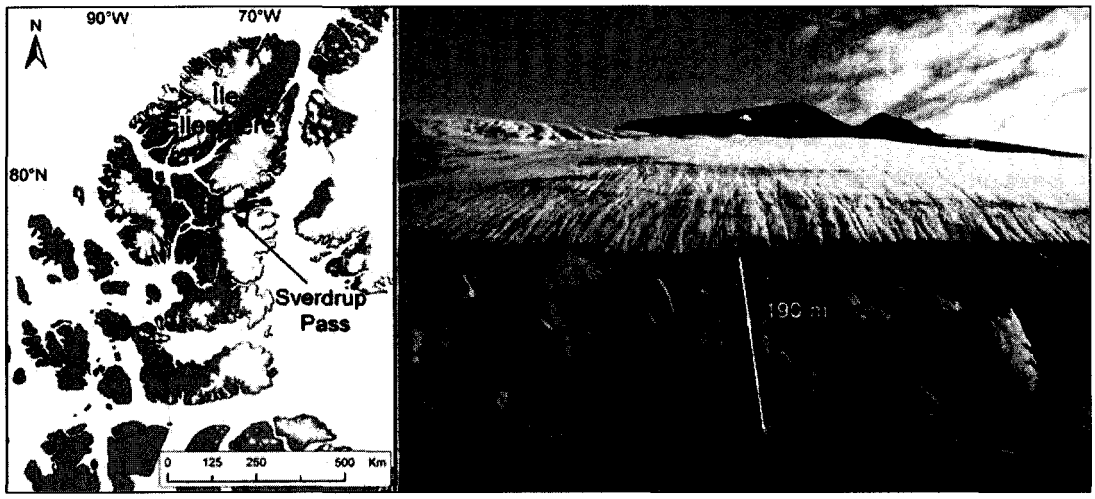

Figure 1.1 Carte de la localisation de Sverdrup Pass sur l'Île d'Ellesmere, Nunavut et photo du terrain proglaciaire à 190 m du front du glacier Teardrop.

Le site d'étude a été sélectionné selon une approche combinant des prélèvements systématiques et semi-aléatoires. Un transect a été établi entre le front actuel du glacier et la moraine terminale du Petit Âge Glaciaire située à une distance de 190 m. Dix-sept sites d'échantillonnage ont été sélectionnés le long du transect. Les sites ont été installés à des distances aléatoires de part et d'autre du transect, du terrain proglaciaire, à intervalle de 6 m le long des premiers 60 m en s'éloignant du front glaciaire puis à intervalle de 20 m jusqu'à la moraine terminale. Trois sites d'échantillonnage additionnels, soit un total de 20 sites, ont été installés au-delà de la moraine terminale à une distance maximale de 212 m du front glaciaire. Les dimensions des sites d'échantillonnage étaient de 40 m x 5 m, le plus long côté étant parallèle au front du glacier. Un minimum de 20 quadrats de 50 cm x 50 cm aléatoirement placés dans chaque site (Figure 1.2 a) a permis de quantifier les paramètres biologiques. Les

analyses détaillées sont basées sur la moyenne des données provenant de ces quadrats. Ces 20 sites ont servi à la caractérisation biotique et abiotique du milieu à partir des prélèvements et descriptions énumérés au Tableau 1.1.

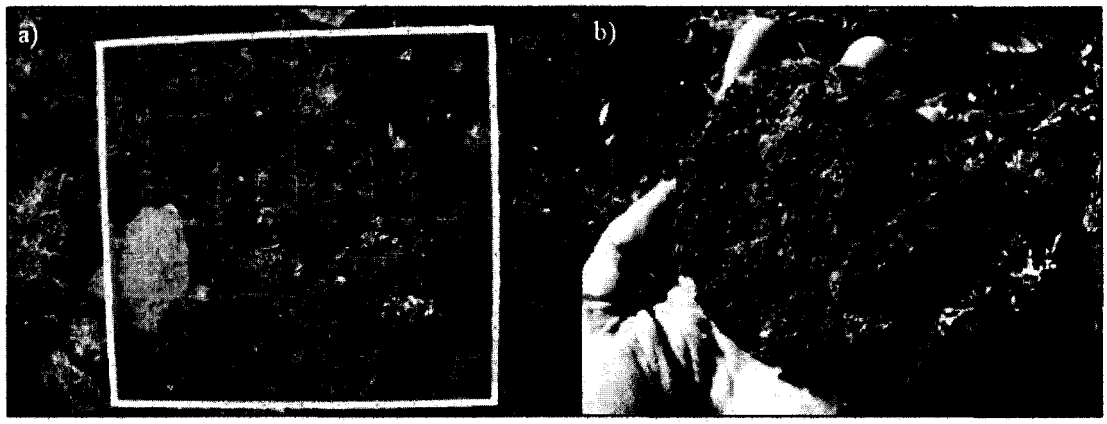

Figure 1.2 a) Quadrat de 50 cm x 50 cm utilisé à chacun des 20 sites pour l'échantillonnage; b) Échantillon de croûte biologique de < 1 cm d'épaisseur prélevé sur le terrain proglaciaire du glacier Teardrop, Sverdrup Pass, Île d'Ellesmere, Nunavut.

À chaque site, dans chaque quadrat de 50 cm x 50 cm, le pourcentage de recouvrement de plusieurs variables biologiques et physiques a été noté, de plus que la richesse spécifique et la densité (nominale et relative) des plantes totales et pour chaque espèce à l'intérieur et hors de la croûte (Tableau 1.1). Les échantillons de sols ont été pris en surface (< 1 cm) et par des carottes de 5 cm de profondeur afin d'analyser les variables physiques et les éléments nutritifs des croûtes et du sol en fonction de la distance au glacier (Tableau 1.1). Ces données ont été utilisées comme variables dans les analyses statistiques multivariées. Une classification divisive (TWINSPAN) a été employée pour créer des groupes de sites et d'espèces selon les correspondances dans les données. Le regroupement des sites a permis de déterminer la succession des groupes de sites en fonction de la distance au glacier. Des analyses canoniques par correspondance (ACC) et par correspondance partielle (ACC partielle) ont été employées afin de déterminer la portion de variance expliquée par plusieurs variables environnementales, notamment la distance au glacier et le pourcentage de recouvrement de croûte.

Les données des échantillons de croûte et de sol employées comme variables dans les analyses multivariées ont été analysées plus en détail afin de séparer les contributions des croûtes et des sols, à < 1 cm et 5 cm de profondeur dans chacun des 20 sites (Figure 1.3). Le recouvrement de croûte, leur épaisseur, le contenu adéquat en eau et la densité brute ont également été mesurés. Une station micrométéorologique a été installée pour quantifier la température atmosphérique à 1.5 m et 10 cm du sol et à une profondeur de 1 cm durant l'été de même que la température, le contenu adéquat en eau, le potentiel hydrique, le carbone organique et la granulométrie à quatre sites à l'intérieur et hors de la croûte (Figure 1.4).

Tableau 1.1 Liste des données amassées pour cette étude dans les 20 sites devant le glacier Teardrop, Sverdrup Pass, Île d'Ellesmere, Nunavut, au cours de l'été 2004.

Variables	Chapitre
Recouvrement (%)	
Plantes vasculaires (total et par espèce)	2
Croûte biologique	2 et 3
Litière	2
Mousses	2
Lichens	2
Eau	2
Fèces	2
Matériel paléo	2
Sol inorganique du glacier (< 0.4 cm)	2
Gravier et petits cailloux (0.4 - 6.4 cm)	2
Les roches (6.4 - 25.6 cm)	2
Les petits blocs (25.6 - 50cm)	2
Les gros blocs et mega-blocs (> 50 cm)	2
Échantillonnage du sol (fraction < 2 mm à 5 cm et/ou 0.7 mm de profondeur)	
Pourcentage de sable	2 et 3
Pourcentage de limon	2 et 3
Pourcentage d'argile	2 et 3
pH	2 et 3
Pourcentage de carbone organique	2 et 3
Pourcentage d'azote total	2 et 3
Parties par million de phosphore disponible	2 et 3
Parties par million de potassium échangeable	2 et 3
Pourcentage de contenu adéquat en eau (fraction totale)	3
Densité brute (fraction totale)	3
Station microclimatologique (capteurs à l'intérieur et hors de la croûte)	
Pourcentage de contenu adéquat en eau	3
Potentiel hydrique (bars)	3
Température du sol et de l'air (+ 10 cm et + 1.5 m) (°C)	3
Richesse spécifique des plantes vasculaires	2
Épaisseur de la croûte (mm)	3
Densité de plantes à l'intérieur et hors de la croûte (totale et par espèce)	
Densité nominale dans et hors de la croûte	
Totale : nombre de plantes individuelles/m^2	2
Reproductive: nombre de plantes reproductives/m^2	2
Rendement reproducteur : nombre d'inflorescences/m^2	2
Densité relative à substrat avec ou dépourvu de croûte	
Totale: nombre de plantes relatives à 100% croûte ou non-croûte	2
Reproductif: nombre de plantes reproductives/nombre de plantes totales/m^2	2
Rendement reproducteur: nombre d'inflorescences/nombre de plantes reproductrices/m^2	2

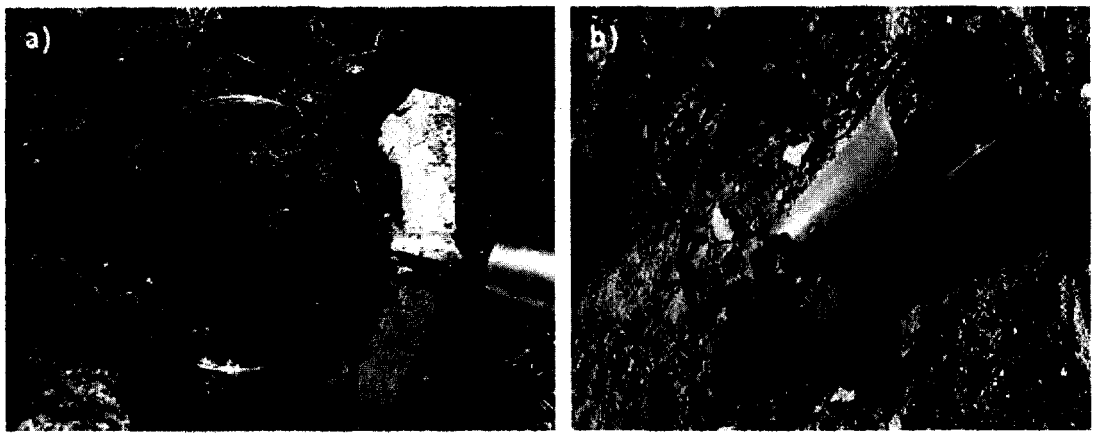

Figure 1.3: Échantillons de a) croûte biologique de < 1 cm d'épaisseur et de b) sol à 5 cm de profondeur prélevé à chacun des 20 sites en avant du glacier Teardrop, Sverdrup Pass, Île d'Ellesmere, Nunavut.

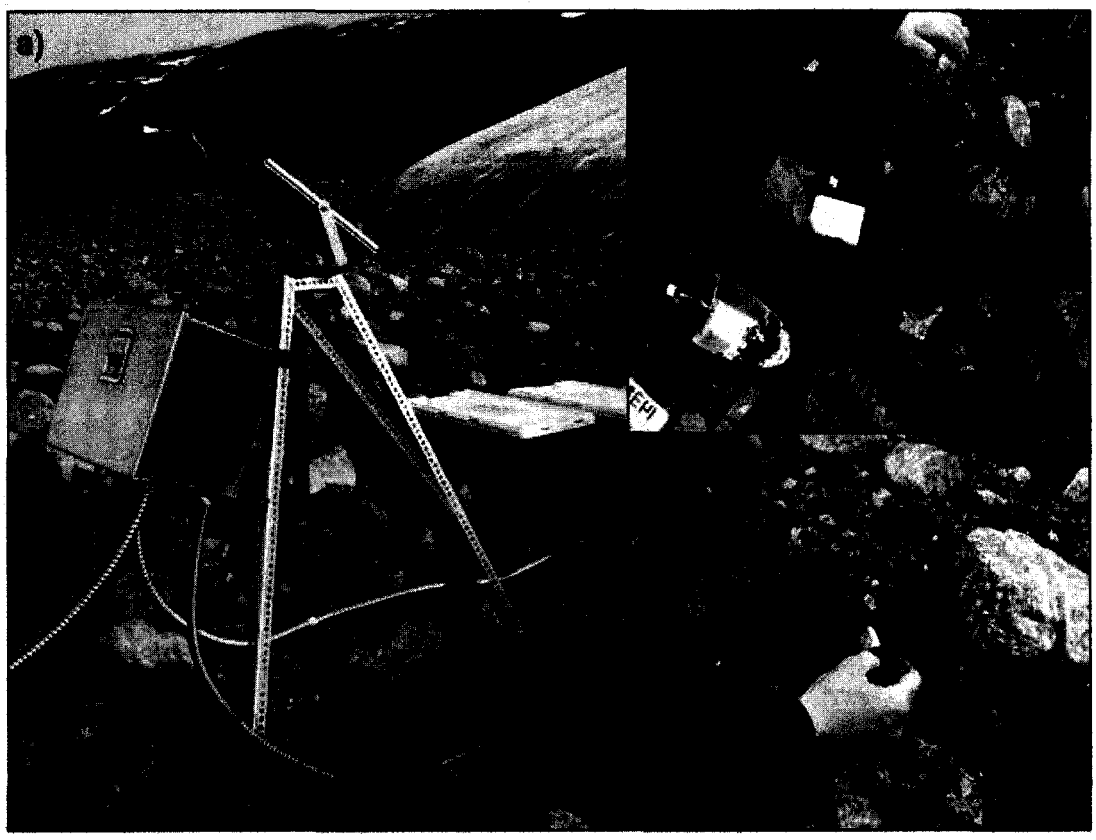

Figure 1.4 La station micrométéorologique (a) et les capteurs placés pour mesurer le contenu adéquat en eau (b) et le potentiel hydrique (c) à l'intérieur et hors des croûtes sur le terrain proglaciaire du glacier Teardrop, Sverdrup Pass, Île d'Ellesmere, Nunavut.

Selon les résultats de l'analyse de classification, les sites ont été divisés en six groupes successionels avec distance au glacier. Ces groupes et le type de substrat (dedans ou hors de la croûte) ont été employés comme facteurs dans des analyses de variance (ANOVAs) unidirectionnelles et bi-directionnelles portant sur plusieurs variables, telles que la richesse spécifique, les densités nominales et relatives, les recouvrements, les propriétés physiques et chimiques de la croûte et du sol, etc. Ces analyses de variance ont permis d'évaluer la relation entre la distance au glacier et/ou du type de substrat pour chaque variable. Des analyses ANOVA suivies par des comparaisons multiples ont été également employées pour déterminer si la distance au glacier entraînait des différences de densité spécifique significatives à l'intérieur et hors des croûtes.

1.5 RÉSULTATS

La végétation le long du terrain proglaciaire est caractérisée par un gradient de complexité croissante qui se traduit par une augmentation générale du recouvrement végétal, de la richesse spécifique et de la densité végétale en fonction du temps. Le recouvrement de plantes vasculaires, la richesse spécifique, le recouvrement de croûtes et les variables abiotiques du terrain étaient statistiquement différentes entre les groupes de classification. Ces différences soulignent les changements qui se sont produits au cours de la succession.

La croissance des croûtes biologiques a commencé environ 2 à 3 ans à la suite du recul du front glaciaire. La superficie maximale occupée par les croûtes a été atteinte en moins de 20 ans. Elle représentait 37 % du milieu soit la majeure partie du substrat disponible pour l'établissement des plantes vasculaires, compte tenu de la grande quantité de cailloux, de roches et de blocs dans le milieu. La colonisation des plantes vasculaires a commencé à moins d'un mètre du front glaciaire. Après ~ 40 ans, à 80 m du front glaciaire, le recouvrement des plantes vasculaires a atteint un maximum de 25 %. Au-delà de la crête de 80 m, sur le reste du terrain et sur la moraine terminale, le couvert végétal s'est stabilisé à environ 20 %. La richesse spécifique s'est également accrue rapidement le long du terrain, de 0 à 21 espèces en moins de 10 ans (18 m du glacier) avant d'atteindre un nombre maximum d'espèces (38) à 160 m du glacier. Parmi les 75 espèces de plantes vasculaires identifiées à Sverdrup Pass par Bergeron et Svoboda (1989), 67 % ont été trouvées sur le terrain proglaciaire. Dans la majorité des 20 sites, la richesse spécifique était généralement plus élevée dans la croûte qu'à l'extérieur de celle-ci bien que les différences n'étaient pas statistiquement significatives.

Les surfaces colonisées par les croûtes biologiques ont soutenu une densité élevée de plantes avec un maximum de 185 plantes/m^2 à l'intérieur de la croûte et 106 plantes/m^2 à l'extérieur de celle-ci. Les densités relatives ont été aussi plus élevées à l'intérieur de la croûte qu'à l'extérieur de celle-ci, mais les résultats n'étaient pas significativement différents. Les densités relatives ont indiqué une relation positive entre les espèces dominantes à longue vie telle que *Saxifraga oppositifolia*, *Salix arctica* et *Dryas integrifolia*. La succession sur le site d'étude procède suivant le modèle de remplacement directionnel de Svoboda et Henry (1987). Ce mode de succession, rare dans le Haut-Arctique, est survenu en raison des conditions abiotiques favorables.

Certaines espèces pionnières telles que *Draba oblongata*, *Saxifraga rivularis* et *Puccinellia bruggemannii*, typiques au sein des sites plus jeunes, ont été remplacées le long de la chronoséquence par des espèces plus tolérantes et ayant une plus grande longévité telles que *Saxifraga oppositifolia* et *Salix arctica.*

Le développement rapide des croûtes biologiques suite à la déglaciation a mené à une accumulation d'azote et de carbone organique dans les croûtes qui s'accorde avec des maximums dans le recouvrement et l'épaisseur de la croûte durant les 20 premières années suivant la déglaciation. Le contenu adéquat en eau, la teneur en azote, en potassium et en carbone organique, le limon et le pH étaient plus élevés à la surface du sol (< 1 cm) qu'à une profondeur de 5 cm. Ceci indique que les croûtes ont fort probablement eu un impact significatif sur le régime d'éléments nutritifs. Les comparaisons des substrats avec et sans croûte démontrent que celles-ci ont un contenu adéquat en eau, une concentration en carbone organique et une fraction d'argile et de limon plus élevée et une densité brute, un potentiel hydrique et une température plus faible comparativement aux sols non-croûtés. Finalement, les analyses statistiques multivariées ont démontré que la distance au glacier et le recouvrement de croûtes étaient les variables les plus déterminantes. Ces deux variables expliquent respectivement 11 et 9 % de la variance dans le recouvrement de plantes vasculaires.

1.6 CONCLUSIONS

Les analyses réalisées au cours de cette étude identifient l'influence directe mais subtile des croûtes sur la richesse spécifique et la densité végétale du milieu proglaciaire. Leur incidence sur la structure de la communauté végétale est beaucoup plus prononcée. Le terrain proglaciaire du glacier Teardrop soutient une communauté de croûtes et de plantes vasculaires bien développée ayant une richesse spécifique, un recouvrement et une densité considérables en comparaison avec d'autres communautés de végétation proglaciaire de l'Île d'Ellesmere. Un apport régulier d'eau de fonte glaciaire a sans doute favorisé le développement rapide des croûtes biologiques en produisant un environnement édaphique avec une humidité et des teneurs en éléments nutritifs élevées. Ces propriétés ont probablement favorisé le taux de succession des plantes vasculaires sur ce terrain. Cette recherche contribue à améliorer notre connaissance limitée du rôle des croûtes biologiques dans l'Arctique et fait la lumière sur les interactions qui opèrent entre les croûtes et les plantes. Compte tenu que l'Arctique est particulièrement affecté par les changements globaux du climat, la fonte qui affecte les glaciers des hautes latitudes offre une occasion privilégiée pour étudier le développement des nouveaux environnements proglaciaires. La recherche sur la facilitation potentielle le long des terrains proglaciaires ajoute à nos connaissances des interactions biotiques le long de gradients environnementaux et pourrait aider à prévoir le potentiel de re-végétation des habitats marginaux et perturbés dans le Haut-Arctique.

CHAPITRE 2

PROGLACIAL SUCCESSION OF BIOLOGICAL SOIL CRUSTS AND VASCULAR PLANTS: BIOTIC INTERACTIONS IN THE HIGH ARCTIC

Katie Breen and Esther Lévesque

2.1 RÉSUMÉ

Notre recherche examine les tendances de distribution des croûtes biologiques et des plantes vasculaires le long du terrain proglaciaire d'un glacier en retrait à Sverdrup Pass, Île Ellesmere, Nunavut, dans le Haut Arctique canadien (79°10'N, 79°45'W), afin d'évaluer l'hypothèse que les croûtes facilitent l'établissement et la croissance des plantes vasculaires durant la succession. Le recouvrement des croûtes biologiques est considéré en ce qui concerne divers paramètres de succès de la végétation : le recouvrement, la composition spécifique, la richesse spécifique, la densité et l'effort reproducteur sur substrat avec et sans croûte biologique. Des analyses multivariées, employées pour examiner des tendances de végétation par rapport à un ensemble de variables environnementales, ont déterminé que la distance du glacier et le recouvrement de croûte étaient les variables les plus importantes, expliquant 11 et 9 % de la variance dans les données respectivement. Les surfaces colonisées par les croûtes biologiques ont soutenu une densité de plantes plus élevée avec un maximum de 185 individus/m^2 dans la croûte et 106 individus/m^2 hors de la croûte. Les densités calculées relatives au substrat disponible (à l'intérieur ou hors de la croûte) révèlent que la densité de plantes tend à être plus élevée dans la croûte cependant ces résultats n'étaient pas statistiquement différents. Les densités relatives ont indiqué des associations avec la croûte pour certaines espèces, en particulier des associations positives avec les espèces les plus dominantes et de longue vie, telles que *Saxifraga oppositifolia*, *Salix arctic* et *Dryas integrifolia*. Les analyses entreprises dans cette étude identifient des influences subtiles mais directes de croûte sur des densités de végétation mais appellent également l'attention sur un effet positif plus grand pour la combinaison de la structure de la communauté. Les croûtes semblent faciliter l'établissement et la croissance des plantes au début et à la mi succession mais peuvent être en compétition pour les ressources disponibles plus loin le long du chronosequence. La succession sur ce terrain proglaciaire suit un modèle de « remplacement directionnel » et soutient une communauté bien développée de croûtes biologiques et plantes vasculaires avec des richesses spécifiques, recouvrements et densités supérieurs comparés à d'autres communautés de végétation proglaciaire précédemment étudiées sur l'Île d'Ellesmere.

2.2 ABSTRACT

Our research examines the distribution patterns of biological soil crusts and vascular plants along the foreland and moraines of a retreating glacier in Sverdrup Pass, Ellesmere Island, Nunavut, in the Canadian High Arctic (79°10'N, 79°45'W), in order to evaluate the hypothesis that soil crusts facilitate the establishment and maintenance of vascular plants during succession. The cover of biological soil crusts is considered with respect to various parameters of vascular plant success; cover, species composition, species richness, density and reproductive effort on substrate with and without biological soil crusts. Multivariate analyses, used to examine vegetation patterns in relation to a set of environmental variables, determined that distance from the glacier and crust cover were the most important variables, explaining 11 and 9 % of the variance in the data respectively. Surfaces colonised by biological soil crusts supported higher plant density with a maximum of 185 individuals/m^2 in crusts and 106 individuals/m^2 out of crust. Densities calculated relative to available substrate cover (in or out of crust) revealed higher vascular plant densities in crust, although results were not significantly different. Relative densities did reveal species-specific associations with crusts, in particular positive associations with the most dominant, long-lived plant species such as *Saxifraga oppositifolia*, *Salix arctica* and *Dryas integrifolia*. The analyses undertaken in this study recognize subtle direct influences of crust on vegetation densities but also draw attention to a larger overall positive effect for community structure. Crusts appear to facilitate plant establishment and growth in early and mid succession but may compete for available resources further along the chronosequence. Succession on this glacier foreland proceeds via a 'directional-replacement' model and supports a well-developed community of biological soil crusts and vascular plants with greater species richness, cover and density compared to other glacier foreland vegetation communities previously investigated on Ellesmere Island.

2.3 INTRODUCTION

Since the end of the Little Ice Age (LIA) ca. 1850, climate warming has led to a decrease in the surface area and mass of many glaciers in the Canadian High Arctic (Dowdeswell, 1995; ACIA, 2005). As glaciers retreat, they expose new terrestrial environments to potential colonisation by microorganisms and higher plants. As colonisation proceeds, a gradient of increasing complexity is created with distance from the terminus of the glacier and the resulting chronosequence is ideally suited to the study of primary colonisation, succession and changing biotic interactions such as facilitation and competition.

Given that true primary colonisation of barren terrestrial environments takes place on the microbial scale, all primary succession should first be viewed as microbial in nature, a fact often overlooked in vegetation studies (Hodkinson *et al.*, 2002). Pioneering organisms such as cyanobacteria, green algae, lichens, mosses, fungi and heterotrophic bacteria are typically the first organisms to colonise the surface and subsurface of exposed soils (Belnap and Lange, 2001). Over time a consortium containing some or all of these microorganisms can create a firm yet flexible organic layer less than 1 cm thick on the soil surface called a *biological* or *microbiotic soil crust* (Evans and Johansen, 1999; Belnap and Lange, 2001). Microbiota present in biological soil crusts can subsist in a variety of extreme habitats worldwide (Belnap and Lange, 2001) including glacier ice (Skidmore *et al.*, 2000; Mueller *et al.*, 2001), whereas vascular plant establishment is more restricted and in the High Arctic favours microsites with higher soil temperatures, lower wind speeds, higher soil moisture content and increased soil nitrate levels (Sohlberg and Bliss, 1984).

Biological soil crusts in temperate ecosystems have been shown to have positive impacts on numerous physical and ecological processes of benefit to vascular plants. Organisms present in soil crusts, such as nitrogen fixing cyanobacteria, have been credited with increasing limiting soil nutrients as well as plant tissue concentration of several essential elements (Harper and Marble, 1988; Belnap and Harper, 1995; Harper and Belnap, 2001). The mucilaginous properties of crusts allow them to retain moisture, reduce the

harmful effects of cryoturbation (Wynn-Williams, 1993; Gold and Bliss, 1995) and protect the soil from erosion by wind and water (Evans and Johansen, 1999; Belnap and Lange, 2001). The darker and occasionally rougher surface created by soil crusts in arctic environments can lower albedo and elevate ambient soil temperatures (Gold, 1998). Although recognized as important contributors to pioneer community development, there is a paucity of information regarding ecological relationships between soil crusts and vascular plants and most published studies relate to temperate desert ecosystems. The most comprehensive study investigating the relationship between vascular plants and soil crusts in the High Arctic took place in a polar desert ecosystem on Devon Island (75°33'N, 84°40'W; Gold and Bliss, 1995; Gold, 1998; Bliss and Gold, 1999), where crusted surfaces were found to support higher plant diversity, biomass, seedling density, organic matter and higher surface and soil temperatures.

With a few notable exceptions, (Tishkov, 1986; Bliss and Gold, 1994; Hodkinson *et al.*, 2003; Jones and Henry, 2003; Okitsu *et al.*, 2004) successional studies on vascular plants in the High Arctic are limited, with research focusing on the succession of vascular plants along glacier forelands or exposed beach ridges. Research on specific plant-crust interactions has, as yet, not been considered during post-glacial succession. General mechanisms of succession such as competition, facilitation and life history traits of individual species all contribute to the pattern and rate of succession but can vary depending on environmental severity (Svoboda and Henry, 1987). While abiotic factors are thought to have the most profound role in structuring extreme arctic plant communities, (Billings, 1987; Svoboda and Henry, 1987; Matthews, 1992) biotic interactions, particularly positive interactions, may play a key role in the structuring of emergent communities which subsist under environmental duress, such as those immediately following the retreat of glaciers. It is generally understood from latitudinal and alpine gradient analyses that the relative importance of positive biotic interactions will increase under increasing environmental stress (Callaway *et al.*, 2002), however such interactions have not been tested on a high arctic glacier foreland. Positive plant interactions, such as facilitation, allow one organism to enhance the establishment, growth or development of a neighbouring organism by a variety of means such as changes in temperature, the accumulation of nutrients, provision of shade, shelter from

wind, changes in albedo and sequestering of propagules (Barbour *et al.*, 1999). While facilitation is generally assumed to occur between two different vascular plants or species, we evaluate the hypothesis that facilitation can also result from biotic interactions between the consortium of organisms comprising biological soil crusts and individual plants or species, producing environmental changes that are favourable for future vascular plants along the chronosequence.

The temporal and environmental gradient created along an arctic glacier foreland presents a unique environment for investigating the relative importance of biotic interactions along a chronosequence and the potential capacity of crusts to facilitate, sustain or interact with the ensuing colonisation by higher plants. Given that high arctic plant establishment is generally favoured by microsites with higher soil temperatures, higher soil moisture content and increased nitrogen (Sohlberg and Bliss, 1984), we hypothesized that soil crusts would offer the biotic input necessary for improving conditions of growth for subsequent vascular plant species and thus increase the rate of succession following glacier retreat. The goals of this paper are 1) to determine whether soil crusts play a role in vascular plant community distribution patterns on a high arctic glacier foreland and 2) if so, to define the general implications of their association with plants across the successional gradient and to determine which biotic and abiotic factors are most important in explaining their distribution patterns.

2.4 MATERIALS AND METHODS

2.4.1 Site description

Field studies were undertaken during the summer of 2004 on the granite-based, north-facing foreland and adjoining older moraine of the 'Teardrop Glacier' (not an official name), situated at the drainage divide of Sverdrup Pass, Ellesmere Island, Nunavut, Canada (79°10'N, 79°45'W; Figure 2.1). Sverdrup Pass is a 75 km-long deglaciated valley running east-west through central Ellesmere Island and is bounded to the north and south by the Agasiz and Prince of Wales Icefields and their numerous outflow glaciers.

The High Arctic is classified as an extreme environment due to its low temperatures, short growing seasons, limited precipitation and nutrient poor soils (Edlund and Alt, 1989) with mean July temperature of 3 - 5 °C and less than 150 mm of precipitation per year (Maxwell, 1981). As such, the vegetation of Ellesmere Island is characterised by sparse polar desert and semi-desert landscapes (Bliss and Matveyeva, 1992) which support low productivity, low plant diversity and 1 - 3 % plant cover, with limited areas supporting 8 - 12 % plant cover (Bliss and Gold, 1999).

The vegetation of Sverdrup Pass has been previously described by Bergeron and Svoboda (1989), Maycock and Fahselt (1992) and the diversity and abundance of soil algae was surveyed by Elster *et al.*, (1999). Sverdrup Pass was classified by Bergeron and Svoboda (1989) as a polar oasis; a rare, isolated, fertile and biologically diverse area with plant cover from near zero to 45 % which supports 75 vascular plant species. While the polar oasis distinction applies primarily to the rich wet meadows in the eastern end of the valley, most of Sverdrup Pass is represented by the more characteristic, extensive polar desert and semi-desert landscapes (Lévesque, 1997).

2.4.2 Glacier retreat in the High Arctic

The recent retreat of high arctic glaciers is attributed to the delayed response to general climatic warming since the end of the LIA (Dowdeswell, 1995) and a significant increase in temperature since 1925 (Bradley, 1990). A terminal moraine 190 m from the June 2004 glacier terminus marks the maximum advance of the Teardrop Glacier during the LIA. The foreland is clearly visible between the glacier and this moraine due to the abundance of large boulders deposited during retreat and the presence of a 'lichen kill zone', where the absence of macro lichens has resulted in a markedly lighter coloured terrain. The only detailed aerial photographic survey of Sverdrup Pass occurred in 1959 (Figure 2.1). Comparisons between air photographs, in combination with *in situ* measurements, allowed Fahselt *et al.* (1988) to determine that the mean annual retreat rate of the Teardrop Glacier was 1.6 m/yr ± 0.1 SE between 1959 and 1986. Measurements taken during the summer of 2004 from a pre-established stake network,

revealed that retreat has increased in recent years to approximately 1.88 m/y (n = 1) from 1987 - 1992 to 2.01 m/yr ± 0.13 SE (n = 7) from 1992 - 2004 (Figure. 2.2).

2.4.3 Sampling design

A benchmark was established on June 29, 2004 at the glacier terminus and all distances referred to in this study are measured from this point of reference. The study area covers the entire foreland length of 190 m from the glacier to the terminal moraine and extends beyond it to 212 m to include an area on older moraines deglaciated at some point prior to the LIA. Due to the large breadth of the glacier terminus (~ 1.2 km across), a 200 m wide sub-section of the foreland was chosen for the study area due to its gentle slope, continuous vegetation and lack of disruptive physical features, such as kames, steep ravines or proglacial lakes that might inhibit the continuous growth of plants and crusts along the foreland.

A north-south transect was marked out perpendicular to the glacier terminus and sites were positioned with increasing distance from the glacier. To capture changes occurring in early community development, sites were placed every 6 m along the transect for the first 60 m and every 20 m thereafter, resulting in 17 sites along the 190 m long foreland. An additional 3 sites were established beyond the terminal moraine (to the north), leading to a total of 20 sites. In order to avoid spatial periodic bias, sites were established at random distances (up to 100 m) alternating to the east or west of the north-south transect line. Sites are generally referred to with respect to their distance from the glacier rather than their terrain age, however approximate ages were determined as seen in Figure 2.2.

2.4.3.1 Vegetation community analysis

At each of the 20 sites, a 40 m x 5 m sampling area was established, with the longest length parallel to the glacier terminus. A general analysis of the site was obtained by randomly placing a 20 m x 5 m plot within the larger 40 m x 5 m site. A more detailed vegetation analysis of each site was undertaken using 50 cm x 50 cm quadrats randomly placed throughout the 40 m x 5 m site. Quadrat number varied between sites since

vegetation cover increased along the length of the foreland, reducing the number of quadrats required to accurately assess vegetation (Lévesque, 1996). A minimum of 30 quadrats were used for each site within the first 54 m of the foreland and a minimum of 20 quadrats were used at each of the remaining sites from 60 m to 212 m. Where sparse plant cover justified it, quadrats were surveyed until a minimum of 20 quadrats containing vegetation were obtained. The detailed and general analyses were compared to ensure consistency of observations. In addition to the species found in the 50 cm x 50 cm quadrats, the entire 40 m x 5 m site area was surveyed for additional species in order to compile a site species list. Vascular plant nomenclature generally follows Porsild and Cody (1980) except for some graminoid (Aiken *et al.*, 2006) and *Draba* species (Mulligan, 1990) and updated nomenclature is included where possible from references currently published by the Flora of North America Editorial Committee (2005).

Within both the 20 m x 5 m plots and the 50 cm x 50 cm quadrats, vascular plant cover was estimated using an abundance scale modified from Lévesque (1996), specifically designed to assess sparse vegetation at 11 levels, (0 %, 0 - 0.5 %, 0.5 - 1 %, 1 - 2 %, 2 - 5 %, 5 - 10 %, 10 - 25 %, 25 - 50 % 50 - 75 % 75 - 90 %, 90 - 100 %). Cover estimates were made using vertical projection to ground level within each quadrat for total and individual vascular plant species as well as for biological soil crust, litter, moss, lichen, standing or moving water, feces and paleo material. 'Paleo material' refers to remnant patches of dead but preserved plant or organic soil matter from earlier interglacial periods occasionally found on high arctic forelands due to the nature of cold-based glacier movement (Bergsma *et al.*, 1984). 'Moss' was determined to be moss that was growing independently of a distinct biological soil crust, either solitary tufts or loose moss carpets. Glacial soil, pebble, rock, small and large boulder cover were also estimated according to a modified Wentworth classification scale (Wentworth, 1922; Table 2.1). The midpoint of each cover value range was used in order to determine the mean of all quadrats per site.

2.4.3.2 Density

Individual vascular plants in the 50 cm x 50 cm quadrats were identified to species level and classified as growing either in or out of biological soil crust in order to determine the total and individual species densities/m^2 as well as species richness in each substrate. The 'outside of crust' category encompassed all alternative substrates in which plants could establish, namely; glacial soil, paleo material, moss, litter and standing or moving water. Species were counted as either individual shoots or clumps depending on specific growth forms (Table 2.2). The true or 'nominal' mean density of plants was first calculated in order to determine the number of individuals present at each site per m^2. Three values were calculated for each of the two substrate categories (in and out of crust): 1) total density: the number of individual plants/m^2, 2) reproductive density: the number of reproductive plants/m^2, and 3) reproductive output: the number of inflorescences/m^2. These densities were calculated for individual species and total vascular plants per site. Data are mean values of all quadrats for each site.

Over much of the Teardrop Glacier foreland, biological soil crusts are the dominant substrate. As a result, a site with a larger cover of crust would have a greater chance of supporting more individuals in the crust simply by chance, given that the crust occupies more space than any other available substrate. In order to compare the mean densities of species or total plants in or out of crust, densities were corrected relative to substrate availability (total density: mean # plants/theorized 100 % cover of each substrate/m^2) or converted to proportions (reproductive density: mean # reproductive plants/total plants/m^2 and reproductive output: mean # inflorescences/reproductive plant/ m^2). The 'outside of crust' cover was determined by adding the cover values of all of the alternative substrates other than crust, listed above, in which vascular plants could establish. These corrected mean density values, referred to from now on as *relative densities*, were calculated for total density, reproductive density and reproductive output for all individual species and total vascular plants per site in and outside of crust.

2.4.3.3 Soil and substrate collections

Soil and surface substrate samples were collected at each site on August 3rd, 2004. Three composite samples of three randomly collected soil cores (6 cm diam., 5 cm deep: 1272 cm^3 total sample) were randomly collected at each site. Samples of biological soil crusts were also collected randomly in each of the sites using an 8.8 cm diameter Petri dish as a core to extract the top 0.7 cm surface layer. Five surface cores were pooled to create one sample per site (8.8 cm diam., 0.7 cm deep: 213 cm^3 total sample). Soil and surface substrate samples were weighed wet to 0.01 g, frozen and shipped at - 10 °C where they were air-dried to constant weight in order to determine volumetric soil moisture content. Texture, pH and nutrient analyses were performed on the < 2 mm fraction of the 5 cm deep soil samples and the 0.7 cm deep substrate samples at the Forestry Soil Science Laboratory, Université Laval, Québec City, Canada. Granulometric analysis (% sand, silt and clay) was determined by the hydrometer method (Bouyoucos, 1962), pH was determined using $CaCl_2$ (McKeague, 1978), organic carbon was determined using methods outlined in Yeomans and Bremner (1988), total nitrogen was extracted by the Kjeldahl method and exchangeable potassium and available phosphorus were determined using the methods in Mehlich (1984).

2.4.4 Data analysis

2.4.4.1 Species-environment relations

A two-way indicator species analysis (TWINSPAN, default settings) (Hill, 1979) was used for classifying the vegetation data set, which consisted of mean cover values for each of the 50 vascular plant species at each of the 20 sites. Cut levels of 0 %, 0.5 %, 1 %, 2 %, 5 % and 10 % were used since the majority of species in the analysis had relatively low mean cover values while a few species had cover values over 5 or 10 %. The minimum group size for division was set at 5.

Mean environmental and species cover data per site were used in ordination analyses using CANOCO 4.53 (Microcomputer Power, Ithaca, NY). A detrended correspondence analysis (DCA) was initially applied to the vegetation data, using default settings, to

determine whether the response was unimodal or linear. Since the first two axes in the DCA had gradient lengths of 3.43 and 1.45 s.d. respectively, a unimodal approach was chosen (Jongman *et al.*, 1995). Canonical correspondence analysis (CCA) was performed in order to relate the environmental variables directly to the species data. Table 2.1 lists the variables applied to initial multivariate analyses, which included one spatial variable, the distance from the glacier (m) and numerous environmental variables. Seven rare species, *Braya glabella, Braya thorild-wulffii, Carex rupestris, Ranunculus sulphureus, Saxifraga hirculus, Saxifraga platysepala* and *Silene acaulis* had minimal cover and occurred either in only one sampling site or within the 40 m x 5 m site area but not within individual 50 cm x 50 cm quadrats and thus were removed from the final analysis while additional rare species were downweighed (ter Braak and Smilauer, 2004). An automatic forward selection of an initial 19 environmental variables resulted in the selection of 9 explanatory variables with conditional probabilities of $p < 0.07$ (Table 2.1). In order to avoid including highly correlated variables, only variables with inflation factors less than 20 were included. The final variables were; distance from the glacier (m), mean percent cover values of crust, glacial soil, paleo material, lichen, moss and litter as well as the phosphorus content (ppm) in soil cores (5 cm depth) and percent nitrogen in surface cores (0.7 cm depth).

In order to separate the variation in the explanatory variables, partial canonical correspondence analysis (partial CCA) was used for selected variables using the variable or variables of interest as predictors and all other variables as designated covariables (Borcard *et al.*, 1992). This method allows for calculation of the proportion of variance uniquely associated with a particular variable or group of variables, in this case the environmental and spatial components as well as the individual contribution of crust cover.

2.4.4.2 Density Analyses

Based on the results of the classification analysis, sites were distinguished into six distance-based groups or successional stages (Figure 2.2). These classification groups served as a proxy for distance or age of terrain in all subsequent analyses. Classification

groups and/or substrate type (in or out of crust) were used as factors in one or two-way analyses of variance (ANOVAs) on species richness as well as nominal and relative total, reproductive and reproductive output densities for all plants, in order to determine the importance of distance from the glacier or substrate type to each variable. ANOVAs were also used to determine whether there were significant species-specific differences in densities in and outside of crust. These were determined for 46 out of the total 50 species that were found in the 50 cm x 50 cm quadrats, (the remaining 4 were only found in the general 40 m x 5 m site area) using the mean densities for each classification group averaged from the original site means. If a species occurred in only one classification group it was tested for substrate effects alone using a one-way ANOVA. Vascular plant and crust cover were tested with a one-way ANOVA to determine differences across classification groups. ANOVAs were performed using Sigma Stat 3.1 (Systat Software Inc., Point Richmond, CA) followed by Tukey multiple comparison tests where appropriate in order to determine where significant differences occurred along the foreland. Whenever data did not meet the parametric analysis of variance assumptions of normality or equal variance, they were rank transformed.

2.5 RESULTS

2.5.1 General vegetation trends

A gradient of increasing complexity was observed in the vegetation along the Teardrop Glacier foreland with a general increase in vegetation cover, species richness and density over time. Of the 75 vascular plant species identified in the polar oasis of Sverdrup Pass by Bergeron and Svoboda (1989), 50 (67 %) were found on the Teardrop Glacier foreland and 51 species were found across both the foreland and old moraine. The complete list of species, representing 14 families is found in Table 2.2. Vascular plant cover, species richness, nominal and relative densities, crust cover and all abiotic terrain features differed significantly across the classification groups ($p < 0.05$) highlighting the changes occurring across the foreland with succession and community development.

The terrain within the first 20 m of the glacier terminus, representing approximately 10 years since deglaciation, was characterised by recently ejected glacial runoff, unsorted

till and intermittent patches of glacial soil and paleo material (Figure 2.3a). Biological soil crusts were rare in this area and when found, were sparse and thin, often appearing as a thin green or black layer on glacial soil or paleo material. As such, the dominant substrates for plant establishment within the first 20 meters of the glacier terminus were glacial soil or paleo material. Approximately 20 m from the glacier terminus, crust cover began to increase and peaked rapidly 36 m from the glacier at 37 % cover (Figure 2.3a), representing the majority of substrate available for plant establishment, given that pebbles, rocks and boulders characterised much of the foreland. Crust remained the dominant substrate across the foreland up to 140 m from the glacier, after which it declined slightly. The decline in crust cover towards the end of the foreland may have been due in part to an increase in standing water and the development of thick moss carpets, which were the dominant constituents of the 'outside of crust' category in these sites. The higher crust cover observed beyond the terminal moraine was likely due to the age and undisturbed nature of the sites as well as low boulder cover, allowing for greater growth of crust.

Vascular plant colonisation began within the first 6 meters of the glacier terminus with the appearance, in the 200 m^2 surveyed, of a single individual of *Alopecurus borealis*. Although vascular plant cover was very low in the newly emerged sites and supported only scattered individual plants with 0.08 % cover, it increased rapidly along the foreland before attaining a peak of 25 % cover 80 m from the glacier (Figure 2.3b). Following the peak at 80 m, vascular plant cover levelled off to roughly 20 % over the rest of the foreland and sites beyond the terminal moraine. Species richness also increased rapidly along the foreland, from 0 to 21 species within 18 m of the glacier (less than 10 years) before attaining a maximum number of species (38), 160 m from the glacier. Species richness was generally higher in crusted substrate in the majority of the 20 sites (Figure 2.4) however there was no significant difference in the total number of species or the relative species richness in and out of crust.

Certain pioneering plant species present in the early successional sites, such as *Draba oblongata, Saxifraga rivularis* and *Puccinellia bruggemannii*, were rarely found in later sites as they were replaced along the chronosequence by long-lived, stress-tolerant

species such as *Salix arctica*, *Cassiope tetragona* and *Dryas integrofolia*. Individual species presence or absence at each site highlights these successional changes (Figure 2.5). Species turnover during succession is also evident among the most dominant species, those with the five highest cover and frequency values across classification groups (Table 2.3). The most common species, with frequency values over 70 % in 3 or more classification groups were *Saxifraga oppositifolia, Luzula confusa* and *Salix arctica.*

2.5.2 Multivariate Analyses

The divisive classification analysis (TWINSPAN) of the cover values of 50 vascular plant species at 20 sites distinguished 8 species groups and 6 site groups at the third level of division. The species groupings 1 - 8 reveal the association of specific taxa with particular successional stages (Figure 2.5). The site groupings reflect distance or terrain age, with the first division (accounting for 29 % of the variance) splitting the foreland at 54 m. Subsequent divisions explained less than 20 % of the variance but separated early and late successional sites into further sequential stages based on terrain age (Figure 2.6).

The canonical correspondence analysis of the same vegetation data set with 9 environmental variables indicated that the community variation seen on this foreland is largely associated with the selected environmental variables in the ordination analyses. The two first axes of the CCA ordination explained 52.5 % of the variation in the species cover from environmental data with a strong proportion on the first axis (38.7 %). The first 4 axes explained 71 % of the variance in species data and 86 % of the variance in the species-environment data, with high species environment correlations. The variance explained by axis 1 and all canonical axes were both found to be significant ($p = 0.001$ each; Table 2.4). The eigenvalue of the first axis was only slightly lower compared to that in the DCA suggesting that most of the variation was kept in the CCA analysis and that the chosen environmental variables explain most of the species variation (Jongman *et al.*, 1995).

The CCA solution is represented in a biplot (Figure 2.7) in which species are displayed according to their affinity towards each other and the environmental variables. Distance from the glacier clearly separates species along the first axis. The cover of surficial paleo material, found predominantly within the first 30 meters of the glacier was associated with early successional species such as *Draba oblongata, Draba cinerea* and *Puccinellia bruggemanni*. These species were generally found within the first 60 m of the glacier in sites with low litter and moss cover. The second axis appears to differentiate two groups of species associated with slightly different late succession habitats. The first group of species, characterized by higher cover of crust, nitrogen content in the top 0.7 cm (crust N) and phosphorus in the top 5 cm (soil P) are all variables that relate to soil and substrate development. This late successional group is composed of species more commonly associated with mature mesic communities and well-developed crusts such as *Cassiope tetragona* and *Dryas integrifolia* (Figure 2.7). The second group of species, characterized by more substantial moss and litter cover and lower soil nutrients are highly associated with older, moist, moss-dominated areas supporting later successional species such as *Carex aquatilis*, *Pedicularis hirsuta* and *Pleuropogon sabinei* (Figure 2.7). This is consistent with observations made in some of the sites at the very end of the foreland, where moss developed to form very wet, thick carpets, unlike the mosses associated with crusts in earlier sites, suggesting that water availability can direct the development of distinct late successional plant communities.

The CCA and partial CCA attributed 82 % of the variance to the selected nine variables ($p = 0.001$), the remaining 18 % of the variation could not be explained by this dataset. The nine variables were further broken down into eight environmental variables and one spatial variable as listed in Table 2.5. The environmental variables alone explained 52 % of the variance ($p = 0.001$). After removing the effects of the environmental variables, distance from the glacier (the spatial variable) was found to explain 11 % of the variance ($p = 0.002$). The proportion of variance explained by crust cover alone was 9 % ($p = 0.003$; '$A^{1'}$ in Table 2.5).

2.5.3 Density

The majority of vascular plant individuals were found growing in crusted rather than uncrusted substrate across the foreland as shown by the three types of nominal mean densities (total, reproductive and reproductive ouput/m^2) per classification group (Figure 2.8 a-c). Total density per site ranged from 0 to 185 plants/m^2 in the crust and 0.1 to 106 plants/m^2 outside of the crust. The density of reproductive individuals in each site ranged from 0 to 60 plants/m^2 in crust and 0 to 21 plants/m^2 outside of crust and the density of inflorescences in each site ranged from 0 to 212 inflorescenes/m^2 in the crust to 0 to 72 inflorescences/m^2 outside of the crust.

Relative densities more accurately consider the cover of available substrate and all subsequent analyses and results refer to relative densities (Figure 2.8 d-f). All three relative densities (total, reproductive and reproductive output/m^2) were significantly different across the classification groups ($p = 0.001$, 0.007, and 0.006 respectively). The total relative plant density was higher in crust in all classification groups, however the preference for crust was not statistically significant ($p = 0.059$). No significant difference was found in the relative reproductive density of plants in or out of crust or in the relative reproductive output density even though 4 out of the 6 classification groups had higher reproductive output in crust than outside of crust.

2.5.4 Individual species densities

Although crusted surfaces generally supported much higher nominal species densities than uncrusted surfaces, when relative densities were considered, only seven species showed significantly different densities and six of these were higher in crust than out of crust, thus any preference for growth in crust appears to be, in part, species specific. Five species were found to have significantly higher total densities in crust than out: *Dryas integrifolia, Salix arctica, Saxifraga cespitosa, Saxifraga oppositifolia* and *Stellaria longipes*, while *Luzula arctica* was marginally significant (Table 2.6). Two species, *Pedicularis hirsuta* and *Saxifraga cespitosa* had higher reproductive densities in the crust. *Dryas integrifolia* had a borderline significant difference in reproductive density whereas *Saxifraga rivularis* was the only species to have a significantly higher

reproductive density outside of the crust. With regard to reproductive output, *Pedicularis hirsuta* and *Saxifraga cespitosa* had significantly higher densities in crust and *Alopecurus borealis* was marginally significant. Although only a limited number of species exhibited a significant difference in density in or out of crust, those species with higher densities in crust were among the most common and dominant species observed on the foreland (Table 2.3), characteristic of mature, mesic arctic environments (Bliss and Matveyeva, 1992). Multiple comparison tests (Tukey) following two-way ANOVAs of species densities highlight where density was positively associated with crust along the foreland (Table 2.6). The results show that most species exhibiting a greater density in crust appear to show this distinction primarily in mid or later successional sites (classification groups 3 – 6) where they have established populations spanning these groups.

2.6 DISCUSSION

2.6.1 General vegetation trends

Previous surveys of glacier forelands on Ellesmere Island undertaken by Jones and Henry (2003) and Okitsu *et al.*, (2004) as well as personal observations of other forelands, suggest that the colonisation and rate of vascular plant succession on the Teardrop Glacier foreland is exceptionally high. Despite its recent release from glaciation, the Teardrop Glacier foreland supports a vegetation cover, species richness and density more often associated with polar oases or richly vegetated areas not affected by the LIA neoglaciation.

The change in vascular plant cover observed across the Teardrop Glacier is somewhat sigmoidal in form, a tendancy observed on other forelands as well, such as in the Swedish Arctic (Stork, 1963), the Alps (Zollitsch, 1969) and the Canadian Rockies (Sondheim and Standish, 1983) as cited in Mathews (1992). The cover of vascular plants on the Teardrop foreland reached a maximum of 25 % yet never exceeded 15 % on the Twin Glacier foreland in the nearby polar oasis at Alexandra Fiord (78°53'N, 75°55'W; Jones and Henry, 2003). Plant cover on other marginal glacier forelands, in Oobloyah Valley, Ellesmere Island (80°50'N, 82°45'W; Okitsu *et al.*, 2004), the subantarctic

Kerguelen Islands (49° S; Frenot *et al.*, 1998) and Iceland (65° N; Arnalds *et al.*, 1987), never exceeded 1 %, 4 % and 10 % respectively. Comparative cover values of biological soil crusts along forelands are limited, however, on a glacier foreland on Svalbard (78°54'N, 12°06'E), Hodkinson *et al.* (2003) noted that crust became apparent 16 years after glacier retreat and reached a maximum of 35 % cover within 60 years, after which time it declined as vascular species colonized the available, stabilized surface. The same study also found high vegetation cover, close to 100 % after 150 years. Our results showed a more rapid rate of colonisation as crusts were visible within 4 years of retreat and attained a cover of 37 % in less than 20 years yet showed a similar, eventual decrease in later successional sites, as vascular plant cover increased.

The high proportion of species colonisation on the Teardrop Glacier foreland, (67 % of the total number of species found in Sverdrup Pass) contrasts markedly with the Twin Glacier foreland, where 94 vascular species have been identified in its surrounding valley (Svoboda and Freedman, 1994) yet only 31 (33 %) of these had colonised the foreland (Jones, 1997). The rate of colonisation was also higher on the Teardrop Glacier foreland with 30 species establishing approximately 15 years after glacier retreat and a maximum of 37 species towards the end of the foreland, compared to a maximum of 24 species after 20 - 30 years of retreat on the Twin Glacier foreland. Species richness on a comparable foreland on Svalbard was also lower, increasing gradually over 100 years and stabilizing with 10 - 13 species. (Hodkinson *et al.*, 2003). Species richness in Oobloyah Valley, Ellesmere Island was extremely low, with a maximum of 6 species found across the LIA chronosequence (Okitsu *et al.*, 2004). The initial peak in richness on the Teardrop Glacier foreland between 20 and 40 m from the glacier (~ 10 - 20 years following glacier retreat) appears to reflect the ability of a large number of species to colonise open spaces in the early stages of succession and also illustrates the overlap in the distribution of early and late colonisers at the same point along the chronosequence.

In addition to species colonisation, the colonisation of individuals, as reflected in the high nominal density values, highlights the successful seed dispersal and/or clonal growth on this foreland. While comparative density values are limited, granitic polar desert sites in the vicinity of the Teardrop Glacier had much lower densities with

averages of 28 plants/m^2 ± 4.3 SE and 3.6 % cover ± 0.8 SE (Lévesque, 1997). Although these sites were higher in elevation, it underscores the successful recruitment and establishment ability on the Teardrop foreland relative to surrounding areas. Colonisation on a foreland is related to the distance from mature resident plant populations (Ryverden, 1971), seed sources and a developing seed bank (Stöckling and Bäumler, 1996), the presence of suitable microsites (Jumpponen *et al.*, 1999) as well as the influence of the glacier on microclimate (Matthews, 1992). Sverdrup Pass is an extremely windy corridor and dispersal is likely achieved through aeolioan transport. Many of the early colonising species were not found on the surrounding older moraines suggesting long distance dispersal. The large boulders scattered across the foreland likely serve as traps for windblown seeds, shelter for existing plants and prevent organic matter and crusts from blowing away. Additional and perhaps significant dispersal vectors on this foreland include numerous grazing and nesting animals, including muskox, lemming, fox and ermine as well as several bird species such as snow bunting, ptarmigan, jaeger and gyrfalcon.

Svoboda and Henry (1987) suggest that despite successful dispersal and colonisation, many plant individuals may not be able to sustain a viable population or progress beyond the initial invasion phase of succession in extreme high arctic environments such as exposed polar deserts (Lévesque, 1997). However, the emergence of species at particular distances along the length of the foreland, as seen in Figure 2.5 is consistent with the 'directional species replacement' model of succession (Svoboda and Henry, 1987), also observed on this foreland by Jones and Henry (2003), whereby species replacement occurs in seral stages with each stage distinguished by a dominant group of species. This model of succession, considered atypical in the High Arctic, is thought to occur due to facilitation and/or competition and is more apt to occur when environmental resistance (*e.g.,* temperature, soil nutrients) is lower than biological driving forces (*e.g.*, germination, establishment ability; see Svoboda and Henry, 1987). The Teardrop Glacier foreland exhibits relatively low environmental resistance due to high water availability, well-developed soil crusts, the presence of paleo material and high nutrient levels (Chapitre 3) as well as shelter from wind provided by the many large

boulders deposited across the foreland, all of which have likely helped vegetation progress well beyond the initial invasion phase of succession.

A considerable cover of biological soil crust, as seen on this foreland, can only develop in sites exposed to adequate surface melt water during the short growing season. Gold and Bliss (1995) suggest that the greater plant community development observed in crusted as opposed to uncrusted sites on Devon Island (75°N) was likely due to the indirect benefit of surface water facilitating the growth, maintenance and nitrogen-fixing activities of organisms in the soil crusts. Even in barren, polar desert environments, species richness and vascular plant cover are much higher in habitats where the soil remains moist for much of the summer and supports a cover of biological soil crust (Bliss and Matveyeva, 1992; Bliss *et al.*, 1994). The Teardrop Glacier is unique compared to many glaciers in the vicinity of central Ellesmere Island in that it supports over 100 small melt water channels evenly distributed across its terminus, averaging 30 - 50 cm across. Although water is available on most glacier forelands as glacial runoff, it is often discharged at such a high rate that it creates one or two large, braided streams that do not provide moisture evenly to all areas of the foreland and can hinder seed establishment and plant growth in areas of high disturbance. The unique melt-patterns on the Teardrop have resulted in a glacier foreland provided with a persistent and even supply of water, often carrying glacial soil, paleo-material and nutrients that encourage colonisation of soil crust microbiota (Elster *et al.*, 1999) and vascular plants.

2.6.2 Plant-crust interactions

While it is widely believed that interactions between plants can change along environmental gradients (Callaway *et al.*, 2002), our results suggest that this tenet may apply to the relationship between vascular plants and crusts along the Teardrop Glacier foreland. In very early succession, within the first few years following glacier retreat, crusts were undeveloped and plant density and cover were too low to be able to detect substrate preferences. However, a general positive association between plants and crusts seems to occur from approximately 20 to 60 m from the glacier as crust cover and vascular plant cover increase in tandem and plant species recruitment is high. Results of

multiple comparison tests revealed that significant species-specific differences in densities in and out of crust became apparent approximately 30 m from the glacier or 15 years after retreat (classification groups 3 - 6; Table 2.6) and that most positive associations with crust occurred for only a handful of species. It is noteworthy that those species that exhibited significantly greater densities in crust were among those with the highest plant cover and frequency, and four out of the five species; *Dryas integrifolia*, *Salix arctica*, *Saxifraga oppositifolia* and *Stellaria longipes* are among the most common arctic species associated with mature, mesic plant communities (Bliss and Matveyeva, 1992). Of these four species, *S. arctica, S.oppositifolia* and *S. longipes* first appeared approximately 20 m from the glacier (~10 years after retreat) and *D. integrifolia* appeared after 60 m but all continued to be dominant members of the community along the rest of the chronosequence, highlighting a positive relationship between crusts and long-lived successional species.

The higher nutrient requirements of later successional species, such as *Bistorta vivipara*, *Cassiope tetragona* and *D. integrifolia* may have delayed their entry but may also have been facilitated in part by their associations with mycorrhizal or free-living bacteria (Hodkinson *et al.*, 2003). These trends concur with the multivariate analyses, which revealed that terrain age, followed by crust cover were the best explanatory variables of community composition. Terrain age and substrate composition have also been shown to play a vital role in vascular plant relationships in temperate deserts where they also promote primarily species-specific responses to crust presence (Evans and Johansen, 1999).

The facilitation of plants by crusts in early succession is likely promoted by high moisture and nutrient levels in crusted soils (Chapitre 3) leading to increased growth of existing plant structures and/or the production of new individuals. The increase in the relative number of inflorescences on plants growing in crust in classification groups 3 and 4 also suggests that crusts provide conditions that encourage reproductive resource allocation, essential for increasing cover and density across the foreland. If colonisation were exclusively age dependent, the number of individuals/m^2 would continue to increase across the foreland. However the total density and cover of plants begins to

stabilize following their respective peaks, approximately 40 and 80 m from the glacier. The high number of individuals seems to ensure the sustained cover but growth limitations appear to exist beyond 80 m from the glacier.

Crusts improve conditions for growth in early and mid succession and continue to be important constituents of late succession communities, however, the increase and subsequent stabilisation of vascular plant cover coincides with a decrease in crust cover, as was also noted on Svalbard by Hodkinson *et al.* (2003). Although rare, competition has been observed in the High Arctic primarily in biotically rich environments, such as wet meadows, or polar oases where vegetation cover can reach 100 % in mature communities (Svoboda and Freedman, 1994). Given the high density and plant cover observed on this foreland, competition between plants and between plants and crust is possible and may occur in late succession due to plants out-competing crusts for limiting resources, including nutrients, ground cover and/or light. For example, the increasing horizontal growth of maturing vegetation such as *Salix arctica,* may compete by physically smothering crusted surfaces. Evans and Lange (2001) suggest that crusts develop best where harsh environments limit the growth of higher plants.

Our results show that plants that can colonize rapidly can take advantage of the superior properties of developing crusts such as increased nitrogen and water retention (Chapitre 3), those that survive will be sustained by these properties but will eventually experience a slower growth rate and those that colonise later may be out-competed by existing vegetation. This is of particular interest for those dominant shrub species that do not recruit easily in other parts of the valley (Lévesque and Svoboda, 1995). Crust may therefore play a crucial role facilitating the establishment of structuring species such as *Salix arctica.* Future work will be required to demonstrate whether willow fields can establish without the presence of a crust, if not, the "greening of the North" predicted by some may not occur if drought prevents the development of soil crusts.

Despite the potential for competition in late succession, as vascular plant cover exceeded that of crusts, the majority of plants were still found to be growing within crusted rather than uncrusted terrain, suggesting that crusts continue to provide a superior substrate for growth despite their eventual decline in cover. The particular significance of crusts to

plants is difficult to identify in later succession given that even plants growing 'out of crust' are still likely benefiting from the ubiquitous presence of surrounding crusts since even the non-crusted areas on this foreland supported higher densities than adjacent polar deserts (Lévesque, 2001). The increase in moss cover in some late succession sites may have occurred when increased moisture conditions allowed mosses to dominate what was previously defined as soil crust.

The trends noted in this study show that crusts can modify vascular plant community structure during succession, however further research is needed to explore the physiological, biochemical and/or ecological relationships between crusts and vascular plants, to determine precise mechanisms of facilitation and/or competition. Field experiments undertaken to test the hypothesis that crusts provide a superior substrate for germination and seedling survival yielded inconclusive results, however the results of laboratory experiments testing germination on crusts collected across the foreland suggest that germination success and leaf growth is greater in plants grown on crusted soils (Annexe 1).

2.7 CONCLUSION

As the Arctic continues to respond to global climate change, (ACIA, 2005) increased melting of glaciers will have consequences for existing and future proglacial community development which will be highly dependent on precipitation regimes and the melt pattern of individual glaciers and ice sheets. As can be seen from the atypical Teardrop Glacier foreland, melt patterns that promote a steady supply of water to new terrain can nurture the colonisation of biological soil crusts which may have subsequent impacts on plant cover, richness, density, biomass accumulation and carbon budgets and as such can promote a "greening of the North". The study of interactions that influence the overall rate and direction of succession will add to our knowledge of the re-vegetation potential of marginal habitats and disturbed areas across the High Arctic.

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Table 2.1 Environmental variables measured at 20 sites on the foreland and adjacent moraine of the Teardrop Glacier, Sverdrup Pass, Ellesmere Island, Nunavut. An automatic forward selection in CANOCO v. 4.35 was used to select variables for further multivariate analyses. The nine most relevant variables with conditional values of $p < 0.07$ (in bold) were chosen for inclusion in the final CCA and partial CCA models. Texture was not included because it was closely related to glacial soil. "N/A" are variables with high inflation factors or covariables (>20).

Variables measured at 20 sites	Conditional p-values
Distance from glacier (m)	**0.002**
Biological parameters:	
Biological soil crust (% cover)	**0.014**
Moss (% cover)	**0.06**
Lichen (% cover)	**0.068**
Litter (% cover)	**0.042**
Feces (% cover)	0.092
Physical parameters:	
Glacial soil (< 0.4 cm) (% cover)	**0.066**
Paleo material (% cover)	**0.006**
Pebbles (0.4 - 6.4 cm) (% cover)	0.14
Rocks (6.4 - 25.6 cm) (% cover)	1
Small boulders (25.6 - 50 cm) (% cover)	N/A
Large boulders (> 50 cm) (% cover)	N/A
Standing or moving water (% cover)	N/A
Volumetric water content (%)	0.098
Analyses of soil fraction < 2 mm:	
Texture 5 cm deep	
Sand (%)	0.05
Silt (%)	N/A
Clay (%)	0.132
Chemistry 0.7 mm deep:	
pH	N/A
C (organic) (%)	N/A
N (total) (%)	**0.006**
P (available) (ppm)	N/A
K (exchangeable) (ppm)	N/A
Chemistry 5 cm deep	
pH	0.1
C (organic) (%)	0.21
N (total) (%)	0.082
P (available) (ppm)	**0.052**
K (exchangeable) (ppm)	0.094

Table 2.2 List of vascular plant species and growth form of plants on the foreland and adjacent moraine of the Teardrop Glacier, Sverdrup Pass, Ellesmere Island, Nunavut. Growth form indicates habit used in density analysis, i = 'individual' or c = 'clump'. [+]Species not found in the 50 cm x 50 cm quadrats but found within 40 m x 5 m site. *Additional species seen on the foreland but not encountered in either 40 m x 5 m site or 50 cm x 50 cm quadrats.

Family and species name and authority	Growth form
Brassicaceae	
Braya glabella Richardson	i
Braya thorild-wulffii Ostenf.	i
Cardamine bellidifolia L.	i
Draba cinerea Adams	i
Draba corymbosa R.Br. ex DC.	i
Draba oblongata R.Br. ex DC.	i
Draba subcapitata Simmons	i
Draba lactea auct. non Adams	i
Erysimum pallasii (Pursh) Fernald	i
Eutrema edwardsii R. Br.	i
Caryophyllaceae	
Cerastium alpinum L. subsp. *lanatum* (Lam.) Aschers. & Graebn.	c
Minuartia rubella (Wahlenb.) Hiern	c
Silene acaulis (L.) Jacq. [+]	-
Silene uralensis (Rupr.) Bocquet subsp. *uralensis*	i
Stellaria longipes Goldie subsp. *longipes*	c
Cyperaceae	
Carex aquatilis Wahl. var. minor Boott	i
Carex fuliginosa Schkuhr.	c
Carex nardina Fries s.lat.	i
Carex rupestris All. [+]	-
Eriophorum angustifolium subsp. *triste* (T. Fries) Hultén	i
Ericaceae	
Cassiope tetragona (L.) D. Don subsp. *tetragona*	c
Juncaceae	
Juncus biglumis L.	i
Luzula arctica Blytt in M.N. Blytt & A.G. Blytt	c
Luzula confusa Lindberg	c
Onagraceae	
Chamerion latifolium (L.) Holub *	-
Orobanchaceae	
Pedicularis hirsuta L.	i
Papaveraceae	
Papaver radicatum Rottb. s. lat.	c
Poaceae	

Alopecurus borealis Trin. subsp. *borealis*	i
Arctagrostis latifolia (R. Br.) Griseb. subsp. *latifolia*	i
Festuca brachyphylla J.A. Schultes ex J.A. Schultes & J.H. Schultes	c
Pleuropogon sabinei R. Br.	i
Poa abbreviata R. Br.	c
Poa arctica R. Br. s. lat.	c
Puccinellia bruggemannii T.J. Sørensen	i
Polygonaceae	
Bistorta vivipara (L.) Gray	i
Oxyria digyna (L.) Hill	c
Ranunculaceae	
Ranunculus sulphureus Sol.	i
Rosaceae	
Dryas integrifolia Vahl.	c
Potentilla hyparctica Malte	c
Potentilla nivea L.	c
Potentilla pulchella R. Br.	c
Salicaceae	
Salix arctica Pall.	c
Saxifragaceae	
Saxifraga cespitosa L.	c
Saxifraga cernua L.	c
Saxifraga foliolosa R.Br.	c
Saxifraga hirculus L.[+]	-
Saxifraga nivalis/tenuis	c
Saxifraga oppositifolia L.	c
Saxifraga platysepala (Trantv.)Tolm.[+]	-
Saxifraga rivularis L.	c
Saxifraga tricuspidata Rothb.	c
Total = 51 species	

Table 2.3 Mean cover and frequency of the five most abundant vascular plant species (highest mean cover and frequency values) in each of the six classification groups surveyed across the Teardrop Glacier foreland and adjacent moraine, Sverdrup Pass, Ellesmere Island. NB: Values are given only for the top five in each classification group. Species may be present in other groups but do not appear in the top five.

	Cover (%)						**Frequency (%)**					
	Classification groups						**Classification groups**					
Species	**1**	**2**	**3**	**4**	**5**	**6**	**1**	**2**	**3**	**4**	**5**	**6**
Papaver radicatum	0.006						1.1					
Saxifraga rivularis	0.002						0.7					
Draba oblongata	0.001						0.4	23				
Saxifraga cernua	0.004	0.20					0.7	39	83			
Alopecurus borealis	0.015	0.52	0.67				2.4	21	57			
Saxifraga oppositifolia		0.32	1.4	2.5	2.1	1.7		45	78	83	75	82
Stellaria longipes		0.18	1.4	0.77					67	65		37
Luzula confusa		0.18	2.9	6.1	2.8			33	96	97	73	
Salix arctica			0.64	7.8	7.7	10.5				92	90	86
Luzula arctica				0.40						70	62	
Dryas integrifolia					1.8	0.8						
Carex aquatilis					1.4	1.5						41
Bistorta vivipara						0.8						44
Pedicularis hirsuta											55	

Table 2.4 Summary statistics from the first 4 axes for indirect (DCA, vegetation data) and direct (CCA, environment and vegetation data) ordination analyses using 20 sites, mean percent cover values of 43 vascular plant species and 9 environmental variables (8 environmental and 1 spatial). *p-value from Monte Carlo test with 999 permutations under reduced model.

Ordination method	**DCA**				**CCA**			
Ordination axes	**1**	**2**	**3**	**4**	**1**	**2**	**3**	**4**
Parameters:								
Eigenvalues	0.391	0.099	0.045	0.012	0.376	0.134	0.106	0.070
Species-environment correlations	-	-	-	-	0.984	0.943	0.912	0.956
Cumulative % variance of species data	38.8	48.6	53.0	54.2	38.7	52.5	63.3	70.5
Cumulative % variance of species-environment	-	-	-	-	47.4	64.3	77.6	86.3
Gradient length	3.430	1.450	1.217	1.988				
Total inertia			1.009				0.972	
Sum of all eigenvalues			1.009				0.972	
Sum of all canonical eigenvalues			-				0.794	
Significance of 1st axis*			-				0.001	
Significance of all canonical axes*			-				0.001	

Table 2.5 Partial CCA variances for 9 variables selected from surveys on the Teardrop Glacier foreland, Sverdrup Pass, Ellesmere Island, Nunavut. The total inertia was 0.972. The eight environmental variables include the % cover of crust, glacial soil, paleo material, lichen, moss and litter as well as the soil phosphorus in the top 5 cm (ppm) and nitrogen content in the top 0.7 cm (%). The spatial variable is distance from the glacier (m).

Environmental				
(A^1)	A	B	C	D
		Spatial		

Variable	Variation explained	% variance explained	significance all axes
A+B+C+D	Total	100 %	
A+B+C	Environmental and Spatial variables	82 %	0.001
A+B	Environmental variables alone	71 %	0.001
B+C	Spatial variable alone (Distance)	30 %	0.001
D	Unexplained variation	18 %	N/A
A	Environment after removing effects of B	52 %	0.001
A^1	Crust variable alone	9 %	0.003
B	Interaction between Environment and Spatial	19 %	N/A
C	Spatial after removing effects of B	11 %	0.002

Table 2.6 Results of two-way ANOVAs on relative species densities (total, reproductive and reproductive output) in and out of crust across six classification groups on the Teardrop Glacier foreland and adjacent moraine, Sverdrup Pass, Ellesmere Island, Nunavut. All species were tested but only those with significantly higher density ($p \leq 0.05$ in bold) in crust rather than outside of crust across all classification groups are listed, with one exception "1", which had a significantly higher reproductive density outside of crust among groups but the multiple comparison test did not detect where this difference occurred. Species with marginally significant results ($p \leq 0.06$) are also listed. Classification group numbers indicate the location (Figure 2.2) of significant results of Tukey multiple comparison tests (* $p < 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$, ns = not significant). All data were rank transformed prior to analyses.

Species name	**Total Density** (# plants/m^2 of available substrate)		**Reproductive Density** (# reproductive plants/ total plants/m^2)		**Reproductive Output Density** (# inflorescences/ reproductive plant/m^2)	
	Across groups	Location and significance level	Across groups	Location and significance level	Across groups	Location and significance level
Alopecurus borealis	ns		ns		0.053	4*
Dryas integrifolia	**0.004**	5**, 6**	0.057	4*	ns	
Luzula arctica	0.055	5*	ns		ns	
Pedicularis hirsuta	ns		**0.003**	5*, 6*	**0.019**	6**
Salix arctica	**0.001**	4*, 5**, 6**	ns		ns	
Saxifraga cespitosa	**<0.001**	3***, 4***	**0.029**	3*, 4*	**0.018**	3**, 4*
Saxifraga oppositifolia	**<0.001**	2*, 3***, 4**, 5***, 6**	ns		ns	
Saxifraga rivularis[1]	ns		**0.027**		ns	
Stellaria longipes	**0.012**	3**	ns		ns	

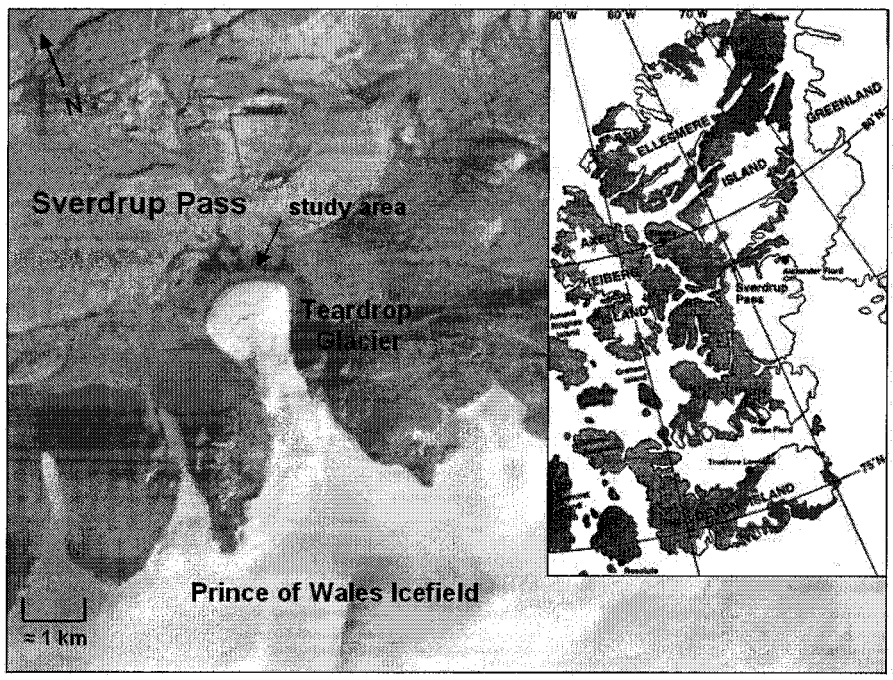

Figure 2.1 Map of Ellesmere Island (inset) and aerial photograph of the Teardrop Glacier in Sverdrup Pass (79°10'N, 79°45'W), Ellesmere Island, Nunavut (National Air Photo Library Natural Resources Canada, 1959).

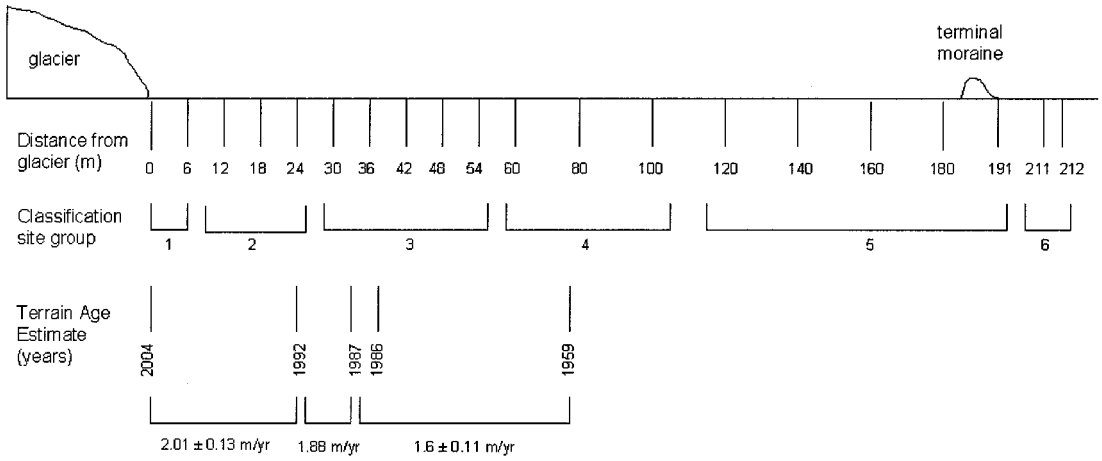

Figure 2.2 The Teardrop Glacier foreland chronosequence, Sverdrup Pass, Ellesmere Island, Nunavut, showing the 20 vegetation sites (identified as distances from the glacier), the 6 derived classification groups and the approximate terrain ages based on measurement of glacier retreat. The terminal moraine marks the maximum extent of glacier advance during the LIA (ca. 1850).

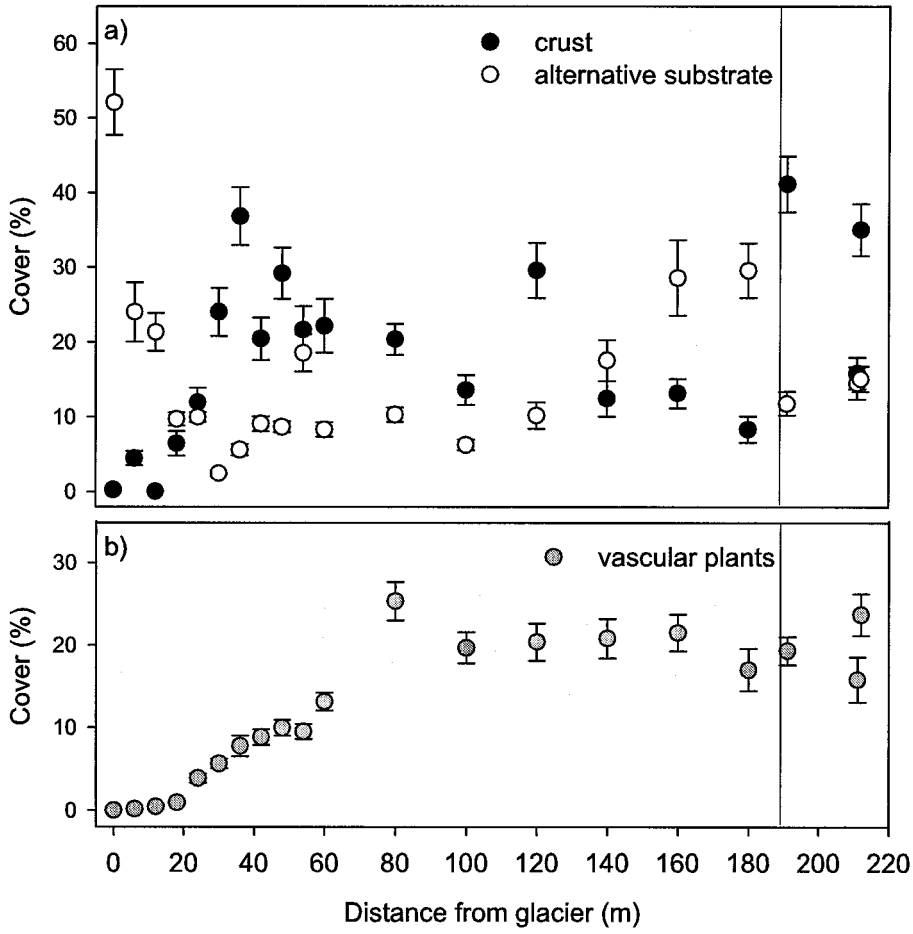

Figure 2.3 a) Soil crust and alternative substrate cover (mean % ± SE) available for plant establishment at each site along the Teardrop Glacier foreland, Ellesmere Island, Nunavut. The alternative substrate or 'outside of crust' category consists of all alternative substrates available for plant establishment (glacial soil, paleo matter, moss, litter and standing water). Pebbles, rocks, small and large boulders are excluded and complete the remaining cover types. b) Vascular plant cover (mean % ± SE) at each site. The solid line indicates the terminal moraine at 190 m.

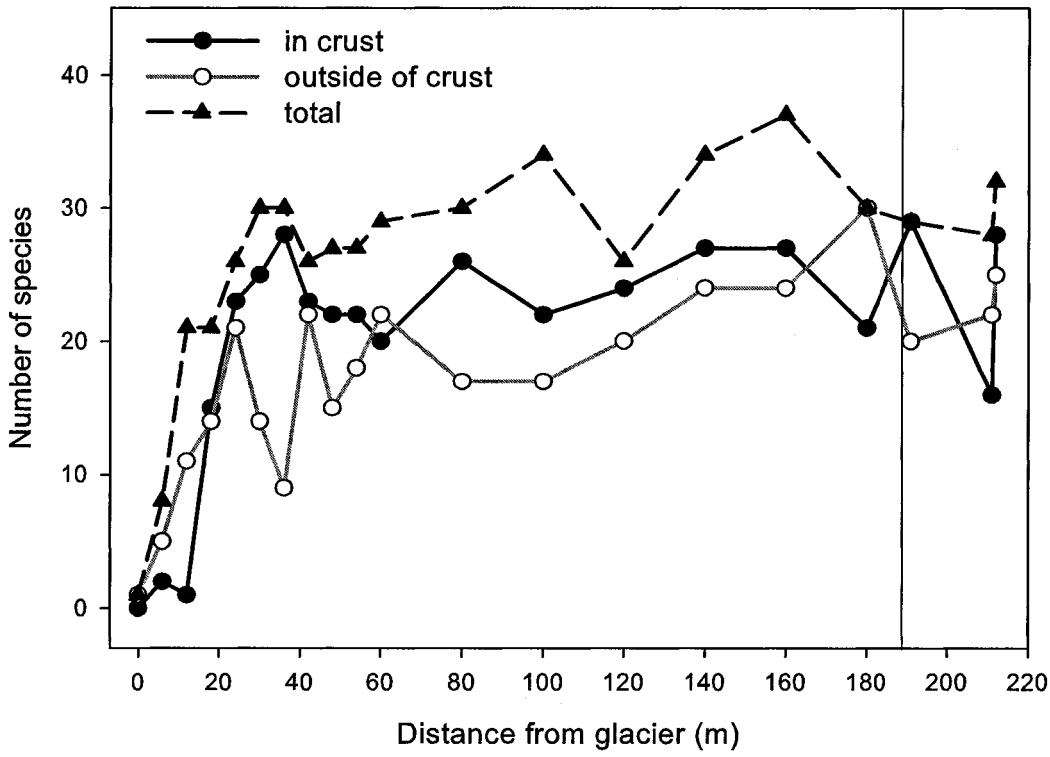

Figure 2.4 Total species richness and number of species growing in or out of crust at each site in front of the Teardrop Glacier, Sverdrup Pass, Ellesmere Island, Nunavut. The solid line indicates the terminal moraine at 190 m.

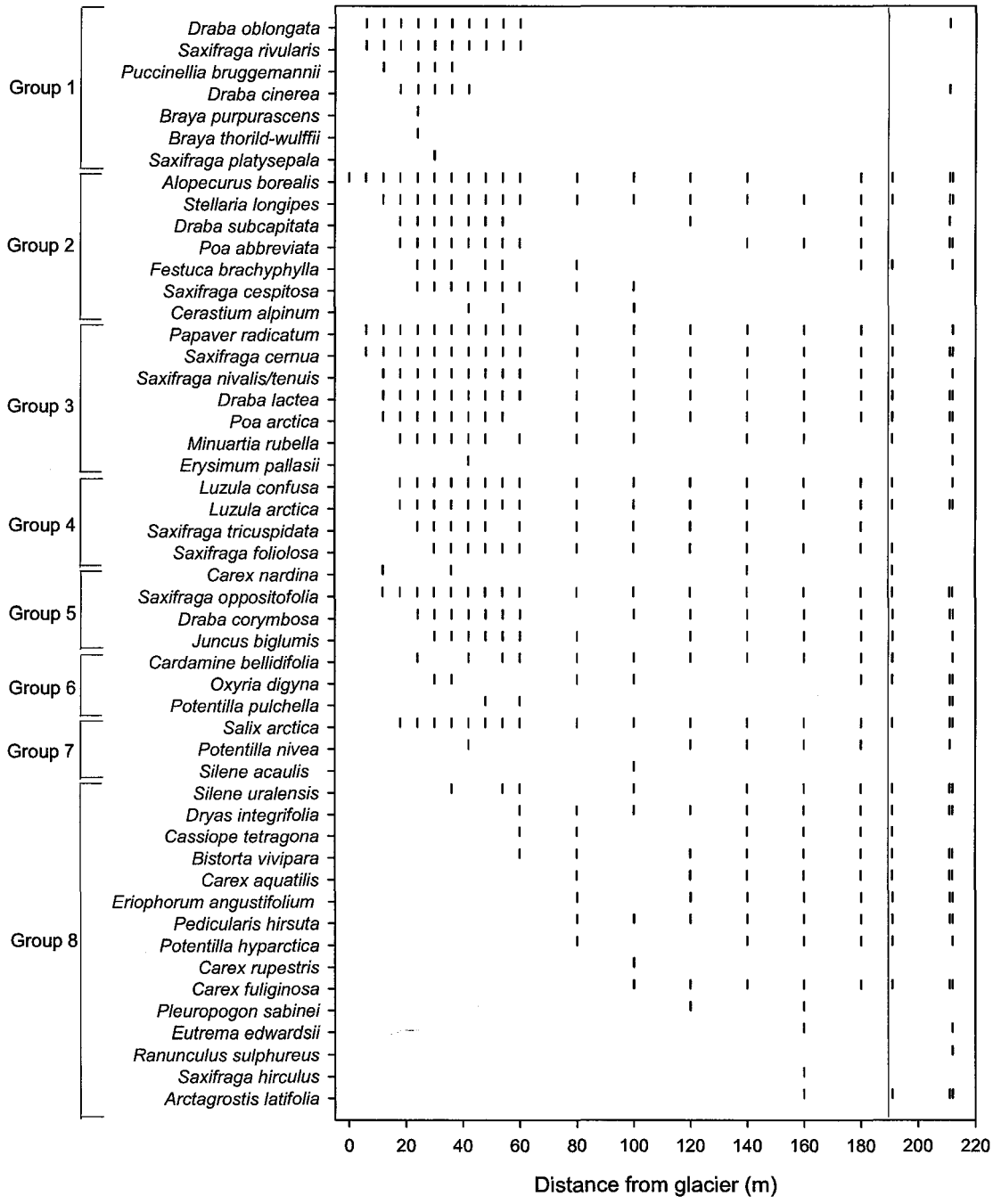

Figure 2.5 Presence of each vascular plant species across the Teardrop Glacier foreland and adjacent moraine, Sverdrup Pass, Ellesmere Island, Nunavut. Species are arranged along the y-axis with respect to their species classification groups (1 - 8). The solid vertical line marks the position of the terminal moraine at 190 m.

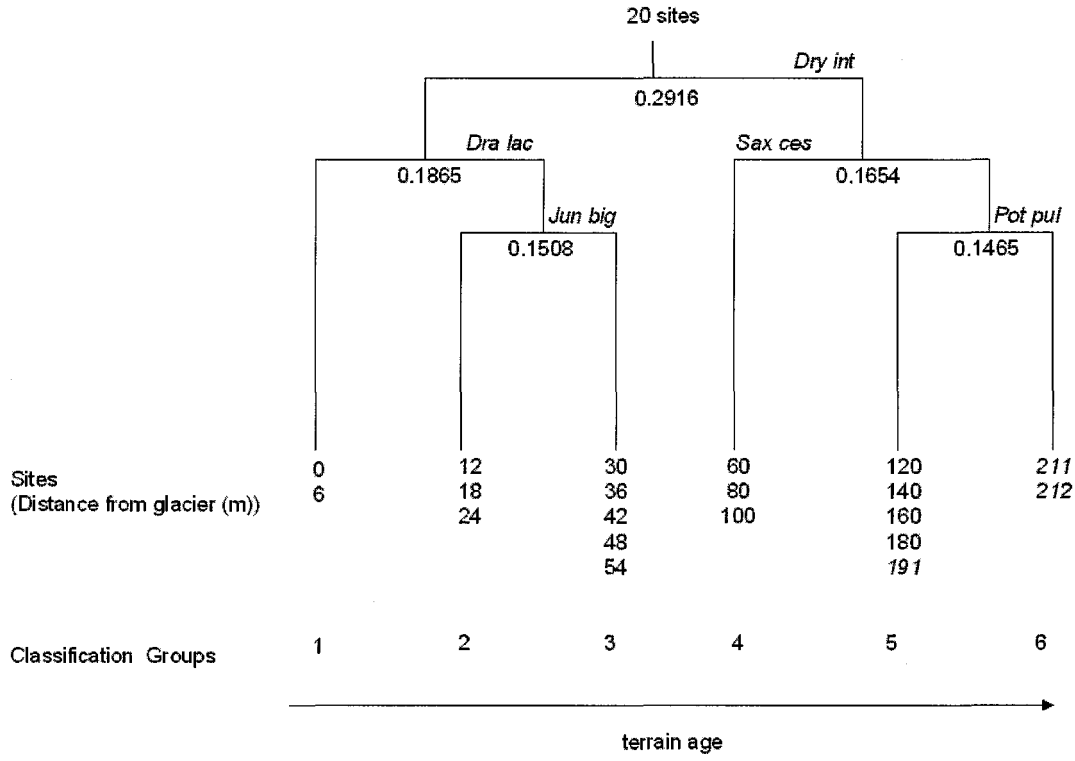

Figure 2.6 Classification dendrogram of vegetation produced from the cover values of 50 vascular plant species across 20 sites in front of the Teardrop Glacier at Sverdrup Pass, Ellesmere Island, Nunavut. Site numbers are distances from the glacier in meters, the three sites beyond the terminal moraine are indicated in italics (*191,211,212*). Eigenvalues and indicator species are identified at each division. Species abbreviations are the first three letters of the species and genus names listed in Table 2.2.

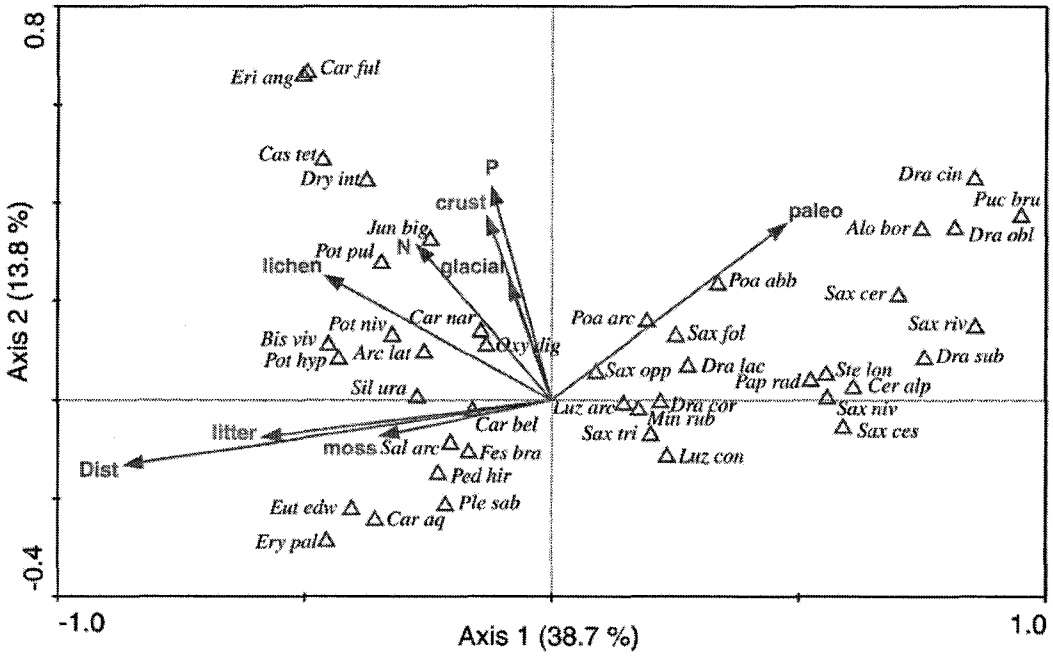

Figure 2.7 Species biplot of the first and second axes of a direct ordination analysis (CCA) of 20 sites, 50 species (triangles) and 9 environmental variables (arrows) sampled along the Teardrop Glacier Foreland, Sverdrup Pass, Nunavut. Environmental variable abbreviations: Glacial, paleo, crust, moss, lichen and litter indicate percent cover of glacial soil, paleo material, crust, moss, lichen and litter, P: available phosphorus concentration in the top 5 cm (ppm), N: total nitrogen in the top 0.7 cm (%), Dist: distance from the glacier (m). Rare species were deleted or downweighed, see text. Species abbreviations are the first 3 letters from the genus and species name listed in Table 2.2.

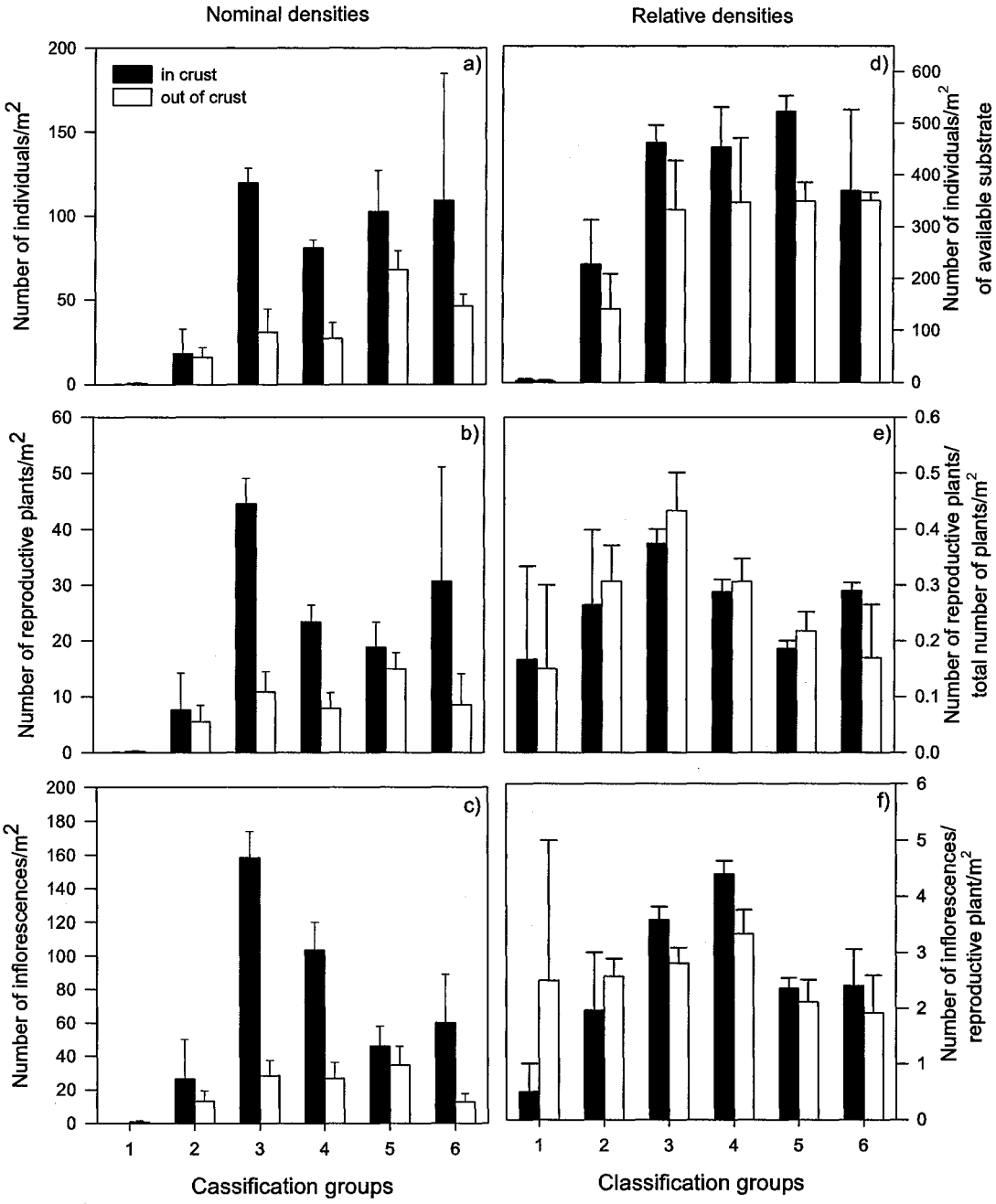

Figure 2.8 Mean nominal (a-c) and relative (d-f) total, reproductive, and reproductive output densities of vascular plants growing in and out of crust in classification groups with distance from the Teardrop Glacier, Sverdrup Pass, Ellesmere Island, Nunavut. Relative densities represent either proportions or the corrected number of individuals that would be present if substrate cover were 100 % in or out of crust.

CHAPITRE 3

THE INFLUENCE OF BIOLOGICAL SOIL CRUSTS ON SOIL CHARACTERISTICS ALONG A HIGH ARCTIC GLACIER FORELAND, NUNAVUT, CANADA

Katie Breen and Esther Lévesque

3.1 RÉSUMÉ

Cette étude examine la relation entre les propriétés physiques, chimiques et microclimatologiques des sols et le développement de croûtes biologiques le long d'un transect de 190 m en marge d'un glacier du Haut-Arctique canadien et d'une moraine adjacente. Nous avons étudié plusieurs propriétés édaphiques (température du sol, teneur volumétrique en eau, potentiel hydrique, teneur en carbone organique, granulométrie, pH, azote total, phosphore et potassium disponible) en surface (environ 1 cm) et jusqu'à 5 cm de profondeur de sols avec et sans croûtes biologiques ainsi que les propriétés dans la croûte en fonction de la distance du glacier. Nos résultats indiquent que la colonisation des croûtes et la stabilisation des sols ont été rapides et que l'accumulation d'azote et de carbone organique correspond à l'épaisseur et au recouvrement maximal de la croûte suivant la déglaciation. La teneur volumétrique en eau, l'azote, le potassium, le carbone organique, la teneur en limon et le pH étaient en général plus élevé dans les échantillons de sols prélevés à moins d'un cm que jusqu'à 5 cm bien que les concentrations variaient en fonction de la distance au glacier. Les surfaces avec croûtes avaient des teneurs volumétriques en eau, en matière organique, en argile et limon supérieures aux sols dépourvus de croûte. D'autre part, la densité brute, le potentiel hydrique et la température étaient inférieurs. Des comparaisons avec les sols de sites analogues dans le Haut-Arctique ont révélé que les concentrations de nutriments étaient élevées. Un apport régulier d'eau de fonte glaciaire a favorisé le développement rapide des croûtes biologiques créant ainsi un environnement édaphique plus humide et plus riche en éléments nutritifs probablement responsable du taux rapide de succession de plantes vasculaires observé sur ce terrain proglaciaire.

3.2 ABSTRACT

This study explores the physical, chemical and microclimatological properties of soils along a 190 m long high arctic glacier foreland and adjacent moraine, in relation to the development of biological soil crusts. We examine various edaphic properties (soil temperature, volumetric water content, water potential, organic carbon content, texture, pH, total nitrogen, available phosphorus and potassium) in surface (< 1 cm deep) and soil (5 cm deep) cores with and without a cover of biological soil crust as well as changes in crust development following deglaciation. Soil crusts developed rapidly following deglaciation and an accumulation of nitrogen and organic carbon in the soil surface coincided with peaks in crust cover and thickness following deglaciation. Volumetric water content, nitrogen, potassium, organic carbon, silt and pH were generally higher in the < 1 cm cores than 5 cm cores yet varied in concentration with distance from the glacier. Crusted surfaces had significantly higher volumetric water content, organic carbon and a greater silt and clay fraction as well as lower bulk density, water potential and temperature compared to uncrusted soils. Comparisons with soils from analogous high arctic sites revealed high nutrient concentrations. A steady supply of water from glacier melt promoted rapid development of biological soil crusts, producing an edaphic environment with enhanced moisture and nutrient properties which likely led to the high rate of vascular plant succession previously observed on this foreland.

3.3 INTRODUCTION

The retreat of glaciers over much of the High Arctic due to climate warming since the end of the Little Ice Age (LIA) ca. 1850, (Dowdeswell, 1995; ACIA, 2005) has resulted in the exposure of new land surfaces for biotic colonisation. Primary succession in the strictest sense occurs on land that is completely devoid of life, and while it is often assumed to be guided by vascular plants, this is rarely the case as microorganisms rapidly colonise even the most extreme terrestrial environments and precede the arrival of most plant colonists (Belnap and Lange, 2001). Proglacial terrain consists primarily of glacial till and infrequent patches of fine sediment or soil supporting scattered individual plants. Although early proglacial environments are generally nutrient-poor, even in seemingly barren environments, nutrients may be obtained through aeolian, terrestrial and fluvial deposition, from subglacial (Skidmore *et al.*, 2000) or supraglacial (Mueller *et al.*, 2001) microbial communities or from relict soil and plant material from previous interglacial periods (Bergsma *et al.*, 1984).

Pioneering microorganisms such as cyanobacteria, green algae, lichens, mosses, fungi and heterotrophic bacteria are typically the first organisms to colonise the surface and subsurface of new terrain and can coalesce over time to form a visible organic matrix on the soil surface known as a biological soil crust (Evans and Johansen, 1999; Belnap and Lange, 2001). Crusts may contain some or all of these organisms, the composition of which varies due to many factors including climate and terrain age (Belnap and Lange, 2001). In polar deserts or recently deglaciated areas devoid of higher plants, soil crust constituents can be the only primary producers and thus represent the trophic base of the developing ecosystem on which heterotrophic components depend (Elster *et al.*, 1999). The early microbial members of a community therefore form a precursor for future soil crust development and are believed to be crucial in laying the foundation of an organic and nutrient-enriched medium in which more complex organisms may become established (Smith, 1991; Wynn-Williams, 1993).

Biological soil crusts can occur in all arid and semi-arid regions but their ecological significance has been studied most extensively in temperate and warm desert ecosystems

around the world. The largest arid regions within Canada are the polar deserts and semi-deserts of the High Arctic which represent 95% of its ice-free terrain (Bliss *et al.*, 1973) and where crusts have been recognized as important contributors to high arctic ecosystems (Sohlberg and Bliss, 1984; Gold and Bliss, 1995; Anderson and Bliss, 1998; Gold, 1998; Bliss and Gold, 1999; Dickson, 2000). Crusts are well adapted to the severe conditions of polar terrestrial environments and are able to survive freezing and thawing, desiccation and rehydration as well as continuous summer solar radiation (Elster, 2002). It is also suggested that the predominance of a darker, rougher soil surface can reduce albedo and substantially elevate arctic soil and surface temperatures (Gold and Bliss, 1995; Gold, 1998).

Arid regions of the world generally lack substantial vegetation cover and soil-stabilizing roots, therefore crusts perform a key role in stabilizing otherwise mobile surfaces and protecting soil from erosion and cryoturbation (Wynn-Williams, 1993; Gold and Bliss, 1995; Evans and Johansen, 1999), of particular importance in the Arctic where soil cover is thin, undeveloped and overlays thick permafrost. The adhesive, mucilaginous properties of several cyanobacterial genera, combined with the rhizoids of mosses and fungal hyphae of lichens further promote consolidation and stability by aggregating soil particles (Belnap and Lange, 2001). Many of the organisms in biological soil crusts enhance soil water retention and nutrients and have been found in temperate deserts to increase plant uptake of bioessential elements (Harper and Marble, 1988; Harper and Pendleton, 1993; Harper and Belnap, 2001). In terrestrial arctic environments plant growth is limited by low nitrogen levels (Henry *et al.*, 1986; Archibold, 1995) and the primary source of nitrogen is fixed by free-living cyanobacteria in soil crusts (Alexander, 1974) therefore small changes in soil nitrogen can be critical to plant community development.

Vegetation community analysis undertaken during the summer of 2004 demonstrated that the Teardrop Glacier foreland in Sverdrup Pass, Ellesmere Island, Nunavut supports a very productive vegetation community with high vascular plant cover, species richness and density and high biological soil crust cover relative to other high arctic glacier

forelands (Chapitre 2). Multivariate analyses in that study found that the distance from the glacier and the cover of biological soil crust were the two most important variables explaining vegetation distribution on the foreland. Since constituents of soil crusts are recognized as facilitators of subsequent vascular plant development, the objective of the present study was to further our knowledge of the edaphic properties of soils colonised by biological soil crusts and to quantify environmental modifications brought about by their development along a chronosequence. We examine the physical, chemical and microclimatological properties of surface (< 1 cm deep) and/or soil (5 cm deep) substrates with and without a cover of biological soil crust at four sites as well as the changes occurring in crusted substrate with time since deglaciation at 20 sites in order to evaluate the hypothesis that crusts modify the edaphic environment in such a way as to enhance the rate of vascular plant succession.

3.4 METHODS

3.4.1 Study Site

The fieldwork for this study was undertaken during the summer of 2004 in the Canadian High Arctic on the granite-gneiss based 'Teardrop Glacier' foreland (79°10'N, 79°45'W), 330 m a.s.l. The Teardrop Glacier is a north-facing outflow glacier of the Prince of Wales Icecap, located at the drainage divide of Sverdrup Pass, a deglaciated valley running east-west across central Ellesmere Island (Figure 3.1). Ellesmere Island belongs to the polar desert vegetation zone (Edlund and Alt, 1989) and lies within the northwestern Arctic climate zone, with a mean July temperature of 3 - 5 °C and less than 150 mm of precipitation per year (Maxwell, 1981). The vegetation of Sverdrup Pass has been previously described by Bergeron and Svoboda (1989) and Maycock and Fahselt (1992) and a survey of the diversity and abundance of soil algae was undertaken by Elster *et al.*, (1999). The Teardrop Glacier foreland is clearly delineated between the glacier's current position and the position of a terminal moraine, marking the maximum advance of the glacier during the LIA. The use of air photos and *in situ* measurements allowed Fahselt *et al.* (1988) to estimate a rate of glacier retreat of 1.6 m/y ± 0.3 SE between 1959 and 1986. *In situ* measurements in 2004 determined that the rate of retreat

had increased to 2.01 m/yr ± 0.13 SE from 1992 - 2004. Retreat rates were used to calculate approximate terrain ages as seen in Figure 3.2.

3.4.2 Sampling design

A 200 m wide sub-section of the ~ 1.2 km wide foreland was chosen for its gentle slope, continuous vegetation and lack of disruptive physical features, such as kames, steep ravines or proglacial lakes that might inhibit the continuous growth of soil crusts or plants along the foreland. Within this sub-section, a reference point was established at the glacier terminus on June 29, 2004, from which all distances referred to in this study were measured. The study area spans the entire foreland length along a north-south transect from the glacier to the terminal moraine (190 m) and extends beyond it to include an area on older moraines deglaciated at some point prior to the LIA (up to 212 m from the glacier).

Sites (40 m x 5 m) were marked every 6 m along the transect for the first 60 m and every 20 m thereafter, resulting in 17 sites along the foreland with an additional 3 sites beyond the terminal moraine, leading to a total of 20 sites (Figure 3.2). To avoid spatial bias, sites were established at random distances up to 100 m alternating to the east and west of the north-south transect line.

3.4.3 Microclimate measurements in and out of crust

A microclimate station was established ~ 40 m from the glacier in order to monitor physical soil variables from crusted and uncrusted surfaces at four sites at 20 m, 40 m, 48 m, and 56 m from the terminus of the glacier (Figure 3.2). Each of the microclimate sites was chosen for its availability of both crusted and uncrusted substrate and its proximity to the microclimate station in order to accommodate a fixed length of cable. A CR10X datalogger and AM416 multiplexer (Campbell Scientific) were used to log hourly and daily averages, minimums and maximums of temperature, water potential and water content in crusted and uncrusted substrate from July 3 to August 7, 2004. Temperature and water potential were measured at all four sites using a soil temperature

probe (Model 107B, Campbell Scientific, accuracy ± 0.2 °C) and a gypsum soil moisture block (Model 223, Campbell Scientific). Volumetric water content was measured at two of the sites (20 and 56 m from the glacier), using a Time Domain Reflectometer (TDR) (CS616, Campbell Scientific, accuracy ± 2.5 % VWC). Instruments were inserted horizontally, ~ 1 - 2 cm below the soil surface, in both crusted and uncrusted surface at each site. The 'in crust' measurements were in fact directly beneath the crusted surface, given that the actual crust is generally less than 2 mm and instrument thickness would not allow for a more shallow measurement, nonetheless the physical properties of crusts are understood to be relevant within the ~ 1 - 2 cm region below the soil surface. Data on ambient air and soil temperature were also collected directly at the microclimate station at 1.5 m and 10 cm above the crusted soil surface and 1 cm below the crusted soil surface using copper-constantan thermocouples.

3.4.4 Surface and soil core sampling

The soil sampling on the Teardrop Glacier foreland was undertaken by distinguishing between 'crusted' and 'uncrusted' surfaces, unless otherwise noted. Crusted surfaces are covered in a visible biological soil crust, usually black in colour, of variable texture and less than 2 mm in thickness. Uncrusted surfaces consist of coarse-textured, grey-coloured, glacio-fluvial sediment, referred to in this study as 'glacial soil', which is more characteristic of arctic forelands (Figure 3.3). A third surface category 'paleo material' is a dark-coloured, organic substrate comprised of dead but intact, relict plant and organic soil matter preserved from a previous interglacial period and released from the retreating ice margin of some cold-based glaciers (see Bergsma *et al.*, 1984). Exposure to weathering leads to the disintegration of most paleo material on the soil surface and therefore it appears to exist only within the first few meters of the glacier, however soil pits dug across the foreland show that paleo material subsists in a patchy network below the surface substrate.

Surface (~ 1 cm deep) and soil (5 cm deep) samples were collected in order to undertake comparative analyses of edaphic properties a) between substrate types (in and out of crust) at four sites and b) within crust among distances from the glacier. Samples varied

in size and quantity between analyses for a) and b). At each of the four microclimate sites, samples in and out of crust were collected on August 7th and 10th, 2004 and consisted of one surface layer (one ~ 15 x 15 x 1 cm deep block (225 cm^3 total sample)) and soil cores from one pooled sample containing three 5 cm deep soil cores (6 cm diam, 5 cm deep (424.11 cm^3 total sample)). The uncrusted substrate at these sites was glacial soil, as described above. The analysis of changing characteristics in crusted soil with distance from the glacier was undertaken using crusted surface (< 1 cm) and soil (5 cm) cores collected on August 9th and 10th, 2004 at a total of 20 sites; 17 sites on the glacier foreland and 3 beyond the terminal moraine, as shown in Figure 3.2. Crusts were collected randomly within unvegetated areas of each site. One surface sample was obtained as a composite sample of five 0.7 cm deep cores collected using the thinner half of an 8.8 cm diameter Petri dish (213 cm^3 total sample). Three soil samples were collected, each a composite sample of three randomly collected 5 cm soil cores (1272 cm^3 total sample). Crusts were thin and undeveloped in the first two sites at 0 m and 6 m from the glacier and as a result paleo material was collected as an alternative to crust.

All soil and surface samples were weighed wet to 0.01 g, frozen and shipped at –10 °C after which they were air-dried to constant weight in order to determine volumetric water content and bulk density. Samples were then sieved and the nutrient and granulometric analyses of the < 2 mm fraction were performed at the Forestry Soil Science Laboratory, Université Laval, Québec City, Canada. The surface samples collected in and out of crust at the microclimate sites were analysed for texture and soil organic carbon (n = 1 in each substrate at each site). A summary of soil variables collected at the microclimatological sites is presented in Table 3.2. The soil (n = 3 per site) and surface cores (n = 1 per site) of crusts from 20 sites with distance from the glacier were analysed for texture, pH, organic carbon, total nitrogen, exchangeable potassium and available phosphorus. Granulometric analysis (% sand, loam and clay) was determined by the hydrometer method (Bouyoucos, 1962), soil pH was determined using $CaCl_2$ (McKeague, 1978), organic soil carbon was determined using methods outlined in Yeomans and Bremner (1988), total soil nitrogen was extracted by the

Kjeldahl method and exchangeable potassium and available phosphorus were determined using the methods in Mehlich (1984).

The physical development of crusts was considered by measuring the thickness of ten randomly chosen crusts at each site and using the mean of the five largest values to estimate a maximum thickness per site. The percent cover of biological soil crust was determined using vertical projection to ground level within a minimum of 20 quadrats (50 cm x 50 cm) placed randomly in each of the 40 m x 5 m site areas to determine a mean per site (Chapitre 2).

3.4.5 Data analyses

At each of the four microclimate sites, multiple one-way analyses of variance (ANOVAs) using Sigma Stat 3.1 (Systat Software Inc., Point Richmond, CA) were performed on ranked data to test differences in and out of crust for temperature, water potential and volumetric water content from logged data as well as volumetric water content and bulk density data determined from surface and soil core samples. ANOVAs were also applied to surface core data to test for differences in texture and organic carbon content in and out of crust.

The 20 sites sampled along the foreland were classified into six groups based on classification analysis (TWINSPAN) of the vascular plant cover previously surveyed at each site (Chapitre 2). These groupings represent distance from the glacier and were used as factors in analyses in lieu of the 20 sites, therefore the average value from each site is used as a replicate within a group. Using the six classification groups, in sequential order relating to distance from the glacier, multiple one-way ANOVAs were performed on soil and/or surface cores to test for the effect of distance from the glacier on pH, organic carbon, nitrogen, phosphorous, potassium, volumetric water content, bulk density, texture and crust cover and thickness.

In all analyses, when data did not meet the assumptions of normality or equal variance, data were either rank transformed or an equivalent non-parametric test was used (Zar,

1999). Multiple comparison tests following ANOVAs were used to determine significant differences between classification groups. The Tukey or Holm-Sidak test was used for parametric data and Dunn's test was used for non-parametric data. Data are presented graphically in relation to classification groups but site values are occasionally noted in the text in order to emphasize maximum or minimum observed values.

3.5 RESULTS

3.5.1 Climate and thawing degree days

The valley of Sverdrup Pass has climatic conditions comparable to the nearby climate station in Eureka, Nunavut (79°58' N, 85°55' W), ~ 150 km northwest of Sverdrup Pass. Over the course of the measurement period from July 3 - August 7, 2004, the mean daily ambient temperature on the foreland, measured 1.5 m above ground, was 5.7 °C and ranged from 2 to 13 °C (Figure 3.4). This was slightly higher than the daily mean July 2004 temperature in Eureka (4.5 °C) but equivalent to July climate normals in Eureka from 1971 - 2000 (Environment Canada, 1971-2000, 2004). Temperature 10 cm above the soil and 1 cm under the soil (with a cover of crust) were warmer on average than air temperature, with daily means and ranges of 6.7 °C (0.2 to 16.7 °C) and 5.9°C (0.4 to 17.4 ° C) respectively (Figure 3.4). July thawing degree-days (TDD) (sum of all daily mean temperatures above 0 °C), estimated from July 3 - August 3 data, reflect this trend with the greatest number of TDD calculated 10 cm above ground (216), followed by 1 cm below ground (190) and 1.5 m above ground (182). These values are comparatively similar to the mean 216 TDD from 1989 - 1993 in the Sverdrup Pass valley 1.5 m above ground (Lévesque *et al.*, 1997) and the mean TDD values from Eureka (178) from 1971 - 2000 (Environment Canada, 1971-2000). Although not recorded at Sverdrup Pass, mean July 2004 precipitation recorded in Eureka was 22.2 mm, almost double the 1971 - 2000 climate normal of 12.5 mm (Environment Canada, 1971-2000, 2004).

3.5.2 Substrate differences in and out of crust

Data logged from instruments placed in and out of crust at each of the four microclimate sites showed that average daily soil temperatures were significantly lower ($p = 0.001$) in crust than outside of crust, ranging from 3.3 °C to 12.9 °C in crust and 3.6 °C to 15.3 °C out of crust (Figure 3.5). As such, noncrusted surfaces had on average, a greater number of TDD in July (282 TDD) as opposed to crusted surfaces (248 TDD; Table 3.1). Water potential was significantly lower ($p < 0.001$) by up to five times, in the crust than out of crust and daily averages ranged from 0.273 to 0.811 bars in crust and 0.262 to 1.453 bars out of crust (a water potential value of 0 bars being equal to pure water; Figure 3.6). An exception to this trend occurred briefly at the 40 m microclimate site which had very undeveloped, thin, dry crust, resulting in a value noticeably closer to the water potential of the uncrusted soil. The volumetric water content measured by TDR at two microclimate sites was significantly greater (up to four times) in crust ($p < 0.001$), with average values of 13.7 % ± 0.5 SE in crust and 9.6 % ± 0.5 SE out of crust (Figure 3.7).

Granulometric analyses of the ~ 1 cm surface cores revealed that soils covered in crust had a greater quantity of silt and clay and were classified as loamy sand while the uncrusted glacial soil was primarily sand, or in the case of one sample, sandy loam (Table 3.2). Organic carbon content in the ~ 1 cm surface cores was significantly greater, by an average of 25 times (Table 3.2). The mean volumetric water content calculated from surface and soil samples taken at the microclimate sites showed a similar trend to data collected by TDR and was significantly greater by up to 15 times in the crusted as opposed to uncrusted surface cores (Table 3.2). The mean bulk density was lower in the crust than outside of crust in both surface and soil cores (Table 3.2).

3.5.3 Changes with distance from the glacier

Biological soil crust cover reached a maximum of 37 % within approximately 20 years of glacier retreat and once established, maintained a thickness of between 1.4 - 1.8 mm (Figure 3.8). Both cover and thickness differed significantly across the classification groups ($p = 0.041$ and $p < 0.009$). After reaching a maximum in cover early in

succession, crust cover declined slightly over the rest of the foreland, yet still represented the majority of substrate available for plant establishment, given that pebbles, rocks and boulders dominate the landscape (up to 44 % cover) and increasing vascular plant growth reduced available terrain for crust establishment (Chapitre 2).

Changes in volumetric water content and bulk density from crusted surface and soil cores across the foreland are shown in Figure 3.9. The average volumetric water content was generally higher in the surface rather than soil cores but there was no significant difference in water content in either across the classification groups (Figure 3.9a). In addition to higher water content, surface cores had a lower bulk density than soil cores, (Figure 3.9b) and both soil and surface cores showed a significant difference in mean bulk density across the classification groups ($p = 0.006$ and 0.002). Surface cores contained on average a greater proportion of silt and less clay and sand than the soil cores with surface core values ranging from 68 - 74 % sand, 16 - 22 % silt and 7 - 12 % clay and in soil cores from 74 - 79 % sand, 11 - 14 % silt and 10 - 14 % clay. Soil texture was relatively homogeneous, only clay varied significantly across the classification groups in the surface cores ($p = 0.030$) and differed mostly in the old moraine sites, which had been exposed to weathering processes and wind deposition for a much longer period of time.

Soil pH and nutrient concentrations changed to varying degrees across the foreland and moraine but were generally higher in the surface cores than in soil cores, with the exception of phosphorus (Figure 3.10). Nitrogen, phosphorus, potassium, organic carbon and pH differed significantly in the surface cores across the site classification groups. In soil cores, all variables except phosphorus and organic carbon were significantly different across the groups. The location of significantly different groups is noted in Figure 3.10.

Previous sampling of the < 2mm fraction of soil from a polar desert granitic gradient in Sverdup Pass (Lévesque, 1997; Lévesque *et al.*, 1997) differed in core depth (10 cm) and altitude (347 - 727 m a.s.l) and provided only a limited quantity (approximately 5 %) of fine fraction soil due to the coarse and rocky substrate but nonetheless offers the

only regional comparative soil values and are thus displayed in Figure 3.10. In general, nutrient values in the surface cores are higher than those obtained by Lévesque (1997) and in the soil cores the differences are less pronounced but are evidently higher for phosphorus and organic carbon (Figure 3.10). The surface and soil cores on the Teardrop foreland generally had a higher proportion of clay and less sand than the surrounding polar desert (Lévesque, 1997).

3.6 DISCUSSION

3.6.1 Substrate differences in and out of crust

The results presented here demonstrate the ability of biological soil crusts, in comparison with uncrusted glacial soil, to alter microclimatological and nutrient regimes, which in turn, create favourable conditions for plant growth. Crusted surfaces would be expected to reduce water stress to plants as a result of increased volumetric water content, organic carbon and lower water potential and bulk density. Lower bulk density is likely indicative of higher organic matter, in this case provided by crust. The unexpectedly lower bulk density values in the soil versus surface cores may point to higher organic matter beneath crusts in the form of paleo material, which would contribute to lower values. Crusted surfaces retained a greater quantity of silt and clay than uncrusted surfaces, which can further contribute to water retention and increase soil fertility since fine, negatively charged clay particles are better able to stick to the mucilaginous sheaths of crusts and subsequently bind with positively charged plant nutrients (Belnap *et al.*, 2001).

The only unexpected result in our analyses came from soil temperature, which was lower in crust, contrary to the results of Gold (1998) and supported on average, fewer thawing degree-days than uncrusted glacial soil. Surface crusts are generally dark in colour and are therefore expected to have a low albedo, absorb radiant energy better than neighbouring uncrusted glacial soil and thus support higher soil temperatures and TDD. Although depth of measurement differed from our study, Gold (1998) found that mean daily soil temperatures 5 cm below crusted surfaces at Truelove Lowland on Devon

Island (75°33'N, 84°40'W) were generally 1 - 3 degrees higher than soil below uncrusted surfaces during sunny periods however during cloudy conditions the difference was negligible. Studies of the water content at that site showed that differences in water content between crusted and uncrusted surfaces was generally less than 5 % (Gold and Bliss, 1995), whereas the difference in water content in the crusted and uncrusted soils on the Teardrop foreland were greater, as was the maximum water content (Table 3.2; Figure 3.7). The summer of 2004 was unusually overcast and rainy in Sverdrup Pass, as evident from the high precipitation recorded in Eureka in July 2004 (Environment Canada, 2004). It is possible that the increased precipitation, combined with predominantly overcast days, increased the water content of crusts and prevented them from receiving sufficient radiation to increase temperatures above those in the adjacent, drier glacial soil. The presence of liquid water in the crusts acts as a buffer to temperature change due to the specific heat capacity of water, thus stabilizing soil temperatures. Water potential and soil moisture data confirm that crusts assure more consistent water availability throughout the summer, despite episodic glacial discharge and decreasing volumetric water content over the summer. Our results show that crusts may not always provide the warmest substrate for plant establishment and that year to year and even daily variations can be weather dependent, as was noted by Gold (1998). However, high soil surface temperatures, of up to 30 °C in the High Arctic, (Gold, 1998) can actually be a source of severe physiological stress to plants in a polar desert environment, especially if water is limiting, as in dry glacial soils where water content was less than 10 % for most of the summer. Despite fewer thawing degree-days, the lower temperatures observed in crust were sufficient for summer growth and may in fact have protected plants from desiccation caused by increased surface temperatures and water deficit.

3.6.2 Changes with distance from the glacier

Direct comparisons of nutrient concentrations on other forelands are difficult due to dissimilarities between environments, sampling strategies and analyses used. Generalizations regarding soil development abound but commonly suggest that organic

matter and nitrogen accumulate and phosphorus, cation concentrations and pH decrease with time since deglaciation (see Walker and del Moral, 2003). The Teardrop Glacier foreland follows some but not all of these trends due to the distinctive nature of the site. Results presented here show that the development of soils in extreme arctic environments is not necessarily confined to physical and chemical processes, as biological soil crusts have a substantial effect on the nutrient regime. The subtleties observed in the upper 1 cm due to the growth of biological soil crusts would have been lost with the analysis of 5 cm cores alone.

3.6.3 Physical changes

A decline in pH with time is assumed to be a universal characteristic of glacier foreland chronosequences (Matthews, 1992) with the increasingly acidic compounds linked to increasing biological activity. The increase in pH on this foreland is likely attributable to wind-blown dolomitic dust driven onto the granitic foreland from the northern side of Sverdrup Pass valley (Lévesque *et al.*, 1997). However, the growth of crusts along the foreland may also have contributed to the increase in pH, particularly in the surface cores, as the presence of photosynthetic crustal organisms have been shown to significantly increase the pH of surrounding media (Garcia-Pichel and Belnap, 1996; Belnap *et al.*, 2001).

Physical differences between surface and soil cores reveal the capacity of crusts to retain water and contribute to a lower bulk density due to increased organic matter from crust development. The low bulk density values close to the glacier may be due to the presence of large amounts of paleo material under the glacial soil, which can contribute substantial organic matter. The higher clay fraction seen in the Teardrop foreland and old moraine soils as compared to soils from the surrounding polar desert (Lévesque, 1997) may have led to preferential colonisation by crust-forming microorganisms (Kaštovská *et al.*, 2005) and increased overall soil fertility.

3.6.4 Nutrient changes

Colonisation by biological soil crusts generally served to increase nutrients in the crust, where the greatest concentration of nutrients were measured, however individual nutrients exhibited varying trends, not only along the chronosequence but with depth of sampling. Although most nutrient concentrations were higher in the surface than in the soil cores, the beneficial effects of organisms found within the top few mm of crust (such as increased N fixed by cyanobacteria) can eventually be transferred down through soil profiles to provide an overall improvement to soil fertility (Elster *et al.*, 1999). Decreases in certain nutrients in later succession, as seen in the soil cores, may be attributed to the uptake and retention of nutrients by vegetation, in particular for limiting nutrients such as nitrogen. Since most roots are established below the crust layer, in certain cases, a loss of nutrients might be observed in the 5 cm core but not in the upper surface core where nutrients are generally more tightly bound in the presence of a crust (Harper and Belnap, 2001). The roots of various plant species occupy different soil layers and will therefore vary in their capacity to utilize resources from the crust. Harper and Belnap (2001) noted that temperate deserts plants with the greatest mineral uptake were those with shallow feeder roots lying within the portions of the soil profile that were influenced by biological soil crusts. Arctic species have relatively shallow root systems due to a thin active layer (Billings, 1987), suggesting that most species would be able to acquire nutrients leached from the crusts.

3.6.4.1 Nitrogen

Most successional studies show a consistent increase in nitrogen concentration through time following deglaciation with a relatively rapid rise in the early stages of succession and a levelling off or slight decrease at a maximum value on older terrain (Matthews, 1992). The relatively high initial N content observed in the two earliest sites (group 1; Figure 3.10) on the Teardrop foreland, particularly in the surface cores, is likely due to the release from decomposition of paleo material, as crusts are still immature and unlikely to be contributing large amounts of N to the ecosystem. As the growth of crust proceeded, N in surface cores quickly reached a maximum, coinciding approximately

with peaks in crust cover and thickness and then levelled off and remained high over the rest of the foreland (up to group 5). The decrease in N in the last two old moraine sites (group 6; Figure 3.10) is likely linked with the decrease in water content, which is essential for maintaining high N_2 fixation rates (Dickson, 2000). The discrepancy between N values in surface and soil cores suggests that most of the N is derived from N_2 fixation by cyanobacteria in the developing crusts. In temperate deserts, between 5 and 88 % of N_2 fixed by *Nostoc* has been shown to leak into the surrounding substrate (Magee and Burris, 1954; Silvester *et al.*, 1996; Belnap *et al.*, 1997) and it is likely that some of the N in lower surface layers was leached from the crusts.

At Glacier Bay, Alaska (58°58'N, 136°04'W), a low-arctic glacier foreland, both Crocker and Major (1955) and Bormann and Sidle (1990) documented a peak in the soil N content in pioneer successional stages and a marked decline in later succession, which was attributed to vegetation uptake. They suggest that the rapid initial accumulation appeared to result from N_2 fixation primarily by *Alnus sinuata* and *Dryas drummondii* on the youngest surfaces which, when decomposed was taken up by the succeeding *Picea* stand. Crusts likely played a similar facilitative role in early succession due to N_2 fixation and the decrease in N seen in soil cores in later succession raises the possibility that it may have been progressively taken up by the increasing vegetation cover (Chapitre 2).

Values from comparative sites suggest that the N concentration and rate of accumulation on the Teardrop Glacier foreland are relatively high. Typical, noncrusted soils of the polar deserts have extremely low concentrations of total soil nitrogen (0.04 %), whereas crusted soils can have more than twice this amount (Gold and Bliss, 1995). Nitrogen concentration on granitic plateaus above the nearby polar oasis at Alexandra Fiord (78°53' N, 75°55'W) and Truelove Lowland on Devon Island both had means of 0.01 % (Bliss *et al.*, 1994) while Lévesque (1997) reported an average of 0.21 % in granitic polar desert sites from Sverdrup Pass. On the Robson Glacier foreland in British Columbia (53°07'N, 119°09'W), mean total nitrogen content reached a temporary steady state at 0.4 % in less than two centuries within the uppermost 15 cm (Sondheim

and Standish, 1983), whereas values from 5 cm cores on the Teardrop Glacier foreland reached a mean value of almost 0.4 % in a little over 10 years.

3.6.4.2 Phosphorus

Data on soil phosphorus content on glacier forelands is limited and the information available points to a variety of patterns and processes (Matthews, 1992). Decreases in P concentration have been noted on other forelands at Glacier Bay Alaska (Bormann and Sidle, 1990) and Alexandra Fiord, Ellesmere Island (Jones and Henry, 2003) and are generally attributed to weathering of the mineral soil over time, uptake by increasingly prevalent plants in later succession or the formation of organic complexes that are unavailable to plants at richer, more productive sites. Muc *et al.* (1994) linked low P availability (1 - 7 ppm) with the high organic content of soils, having observed higher phosphorus values in soils of sparsely vegetated polar deserts (up to 64 ppm). Lévesque and Svoboda (1999) also noted a similar trend of lower P availability in sites with comparatively higher plant cover. This might explain the lower phosphorus values in the organic-rich surfaces as compared to the soil cores, which likely contained a greater proportion of mineral-rich glacial soil under the crust. Our P values did not exhibit a clear pattern across the foreland but were generally higher than those on the Twin Glacier foreland at Alexandra Fiord, which had mean values of approximately 5 ppm from 5 cm soil cores (Jones and Henry, 2003). The Teardrop foreland values were also higher than means from 10 cm soil cores in the granitic polar desert soils of Sverdrup Pass (5.9 ppm) (Lévesque *et al.*, 1997) and Alexandra Fiord which ranged between 3 and 14 ppm (Lévesque and Svoboda, 1999).

3.6.4.3 Potassium

Potassium is generally not considered a limiting factor to plant growth in undisturbed natural ecosystems as it can be leached from dead and living tissues (Brady and Weil, 1999). Potassium levels rose steadily across the foreland within both soil and surface cores but crusts appear to enhance the accumulation of exchangeable K as the surface cores reached a maximum of almost 350 ppm in one site, approximately three times

higher than the maximum soil core values. The concentration of P on the foreland was considerably higher than the maximum of 60 ppm in 5 cm soil cores on the Twin Glacier foreland at Alexandra Fiord (Jones and Henry, 2003) and the mean of 24.8 ppm in the granitic polar deserts in Sverdrup Pass (Lévesque *et al.*, 1997).

3.6.4.4 Organic carbon

Richly vegetated areas with soils high in organic carbon are extremely rare and erratically distributed on Ellesmere Island (Tedrow, 1977). Although the organic carbon in soil cores did not show a clear trend with distance from the glacier, the rapid accumulation and subsequent decline of organic carbon in the surface cores coincides with peaks in crust cover and suggests that much of this carbon is derived from crusts. All crust components secrete extracellular carbon within a few days of acquisition and in cyanobacteria, these secretions can represent up to 50 % of total fixed carbon (Lewin, 1956; Fogg, 1966). The organic carbon in both soil and surface cores surpassed the mean value found by Lévesque (1997) in the polar deserts surrounding Sverdrup Pass (Figure 3.10) as well as that found on alpine moraines in front of the Robson Glacier, British Columbia, which had a maximum of 0.87 % at 15 cm depth after 100 years (Sondheim and Standish, 1983).

In temperate deserts, studies have shown that crusts appear to consistently enhance uptake of elements such as N, K and several micronutrients and to occasionally reduce uptake of other essential elements such as P (Harper and Belnap, 2001). While our results for N, P and K seem to follow the same trend, results are likely site specific and a greater understanding of arctic biological soil crusts is necessary to determine whether there is any validity to these patterns. Future studies in the field and laboratory are needed to determine the rates at which limiting nutrients present in crust can be acquired by vascular plants and incorporated into their tissues.

3.6.5 Additional organic inputs

The influence of paleo material on modern plant community mineralization and decomposition rates has yet to be explored but Jones and Henry (2003) highlighted their importance in dictating plant distribution patterns in early succession. In Sverdrup Pass, paleo material was only evident intermittently within the first 30 m of the glacier, after which time it was either buried by glacial soil and debris or degraded by exposure to sun, wind or glacial runoff. However soil pits dug across the foreland and on the older moraine beyond the foreland clearly showed patchy but distinct layers of paleo material that have likely been contributing to the surrounding nutrient and organic matter pool since initial LIA deglaciation. The high concentration of nitrogen and organic carbon close to the glacier also suggests the input of nutrients from organically rich paleo plants and soils. Paleo material likely provides nutrients to microorganisms and plants throughout succession however a more detailed analysis of past deposition layers would be required to quantify its precise contribution. Other sources of nutrients on this foreland include feces from numerous animals, including muskox, lemming, fox and ermine as well as several bird species such as snow buntings, ptarmigan, jaegers and gyrfalcon. Multivariate analyses of above-ground cover did not find feces to be a significant determinant of vegetation distribution (Chapitre 2) yet it likely contributes to below ground nutrient pools. Researchers of temperate desert crusts have raised the possibility that plants grown on crusts provide better quality forage for grazing animals (Robbins, 1983; Harper and Belnap, 2001), an idea which merits consideration in the Arctic, in particular in view of the high grazing pressure by muskox in Sverdrup Pass (Raillard, 1992).

3.7 CONCLUSION

Since microorganisms within crusts can establish on even the most barren substrates, nutrient rich environments do not preclude their formation, but the increased moisture, exposure to light and fine substrate likely encouraged greater microbial colonisation of crust constituents. The melt pattern of the Teardrop Glacier is unique in that it supports over 100 small melt water channels evenly distributed across its Teardrop shaped

terminus. As a result, water is discharged relatively evenly, providing the foreland with a persistent supply of water, often carrying glacial soil, paleo-material and nutrients that encourage colonisation of soil crust microbiota (Elster *et al.*, 1999). Prolonged surface water flow provides favourable conditions for the proliferation of crust constituents, especially nitrogen-fixing cyanobacteria, principally *Nostoc commune* (Dickson, 2000) which is often the only significant source of nitrogen in extreme polar environments and one of the most limiting nutrients for plant production and community development (Henry *et al.*, 1986). The importance of biological soil crust growth and N_2 fixation was emphasized in previous multivariate analyses on this foreland (Chapitre 2), which showed that the nitrogen concentration and percent cover of crusts were highly significant in explaining the vegetation distribution across the foreland.

A slow rate of succession, in terms of recovery time and species turnover is considered typical in extreme environments like the High Arctic; however, the rate of succession has been shown to increase with higher soil fertility and soil moisture (Prach *et al.*, 1993). The contribution of crusts to the physical environment and nutrient regimes likely led to the increased vascular plant cover, richness and density as well as the increased rate of succession observed on this foreland (Chapitre 2). As global warming increases glacial melt in the High Arctic (ACIA, 2005), glacier forelands will become increasingly important components of polar nutrient regimes and those with the ideal combination of abiotic conditions will be able to support rich biotic communities despite rigorous surrounding environments.

3.8 ACKNOWLEDGEMENTS

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Technologies and the Northern Scientific Training Program. The Polar Continental Shelf Project provided logistical support for fieldwork in the Arctic.

Table 3.1 Thawing degree-days (TDD) in and out of crusted soil in front of the Teardrop Glacier, Sverdrup Pass, Ellesmere Island. July TDD are calculated from July 3 to August 3, 2004.

Distance from the glacier (m)	July* TDD (d > 0 ° C)	
	In crust	Out of crust
20	221	262
40	269	288
48	235	271
56	266	305
mean	*248*	*282*

Table 3.2 Soil characteristics (mean ± SE) of variables from ~ 1 cm deep surface cores and 5 cm soil cores collected in and out of crust at each of the four microclimate sites in front of the Teardrop Glacier, Sverdrup Pass, Ellesmere Island, Nunavut. Significance of difference in and out of crust* $p < 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$. ns = not significant, - = does not apply in the category. Samples are analysed from the fine soil fraction (< 2 mm), except for volumetric water content and bulk density, which are based on the whole sample.

Variables	Surface cores (~ 1cm)		Significance	Soil cores (5 cm)		Significance
	In crust	Out of crust		In crust	Out of crust	
Texture						
% sand	74 ± 1.4	90.3 ± 1.4	***	-	-	-
% silt	16.5 ± 1.8	3.25 ± 0.9	*	-	-	-
% clay	9.5 ± 0.65	6.5 ± 0.5	*	-	-	-
Textural class	sandy loam	sand or loamy sand	-	-	-	-
Organic carbon (%)	4.6 ± 0.9	0.18 ± 0.04	*	-	-	-
Volumetric water content %	44.6 ± 15	2.88 ± 0.20	*	22.5 ± 3.0	13.3 ± 1.4	*
Bulk Density (g/cm^3)	2.4 ± 0.19	4.0 ± 0.32	**	1.19 ± 0.09	1.87 ± 0.31	ns

Figure 3.1 Photograph of the north-facing Teardrop Glacier with arrow indicating the study area and map of Sverdrup Pass in central Ellesmere Island (79°10'N, 79°45'W), Nunavut.

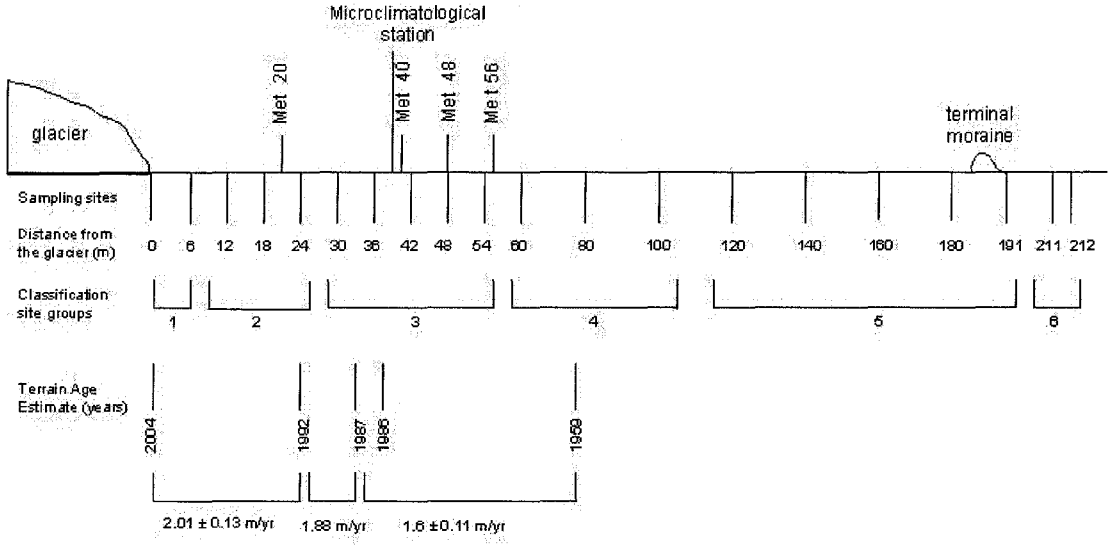

Figure 3.2 Location of the four microclimate and 20 sampling sites, the six classification groups derived from divisive classification analysis and approximate terrain ages along the Teardrop Glacier foreland, Sverdrup Pass, Ellesmere Island, Nunavut.

Figure 3.3 Samples of biological soil crust (left) and glacial soil (right) from the Teardrop Glacier foreland, Sverdrup Pass, Ellesmere Island, Nunavut.

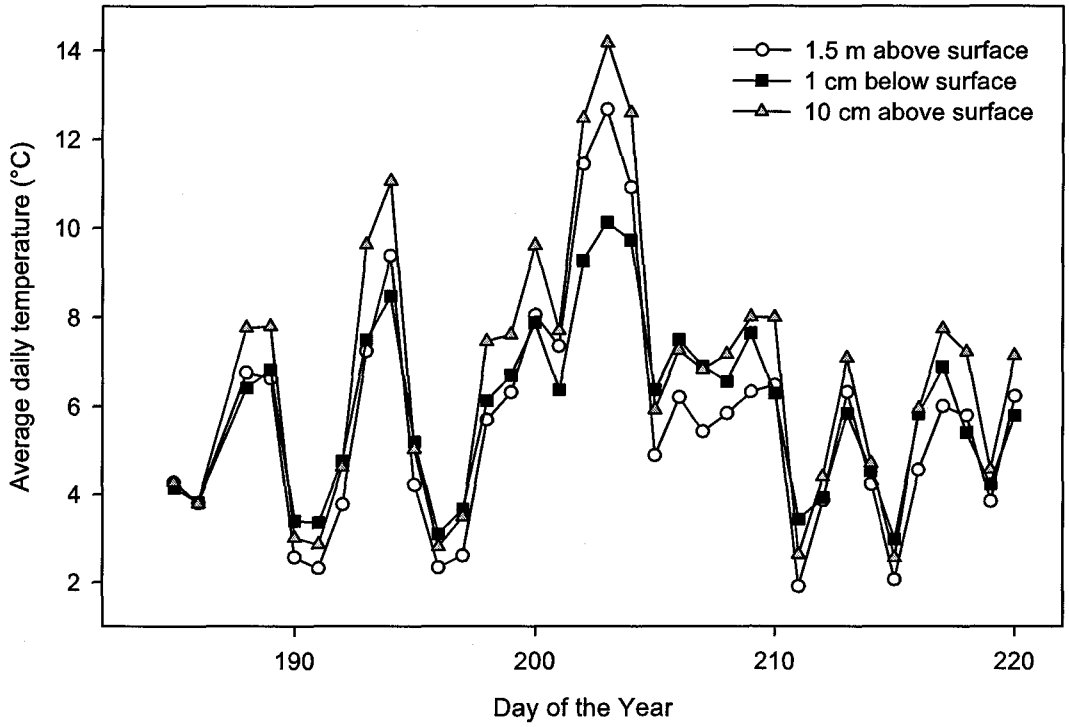

Figure 3.4 Daily mean temperatures at the microclimate station, 40 m from the Teardrop Glacier, Sverdrup Pass, Ellesmere Island, Nunavut from July 3rd to August 7th, 2004.

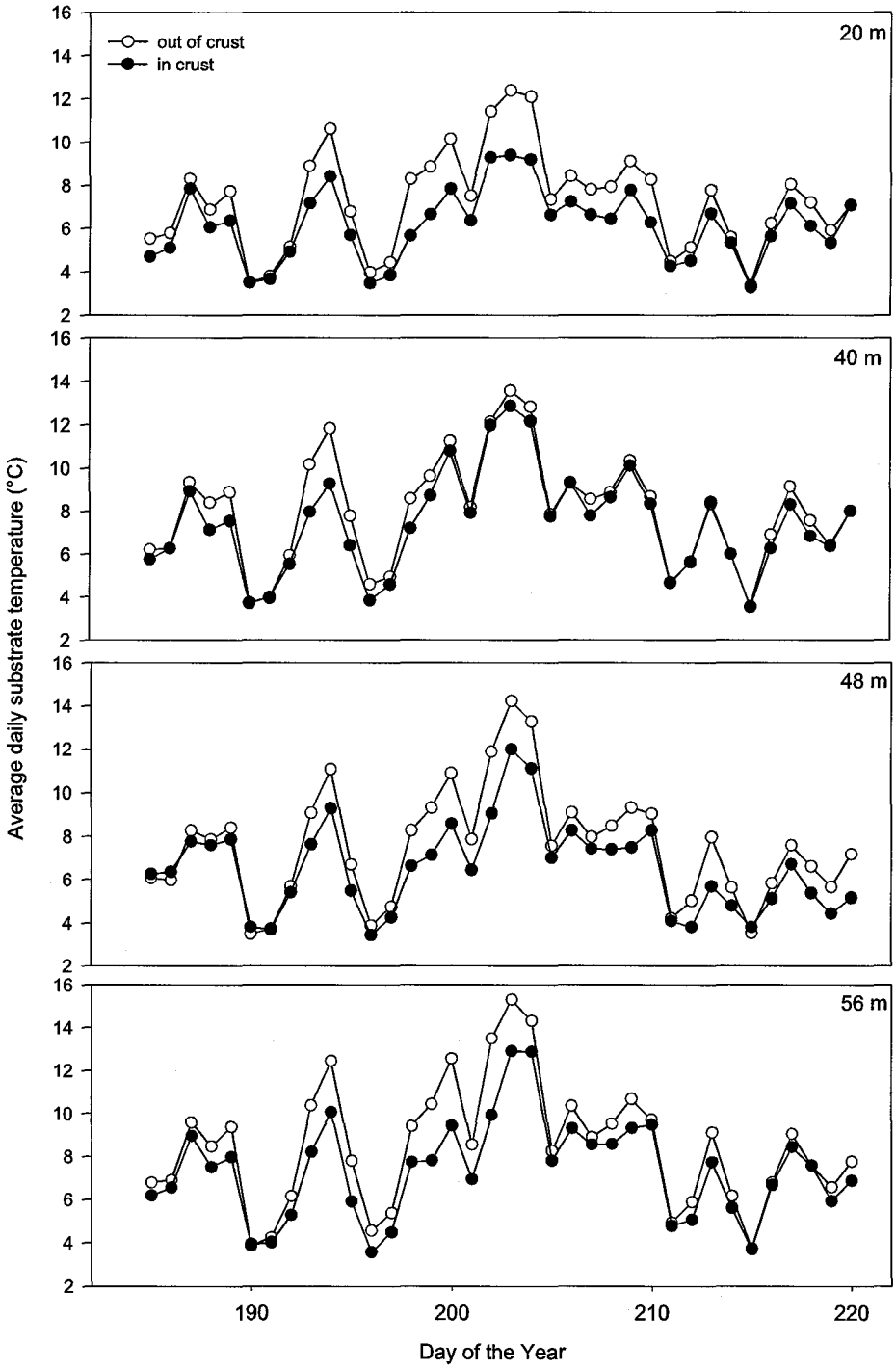

Figure 3.5 Daily mean temperature (°C) of crusted and uncrusted surfaces at each of the four microclimate sites in front of the Teardrop Glacier, Sverdrup Pass, Ellesmere Island, Nunavut from July 3rd to August 7th, 2004.

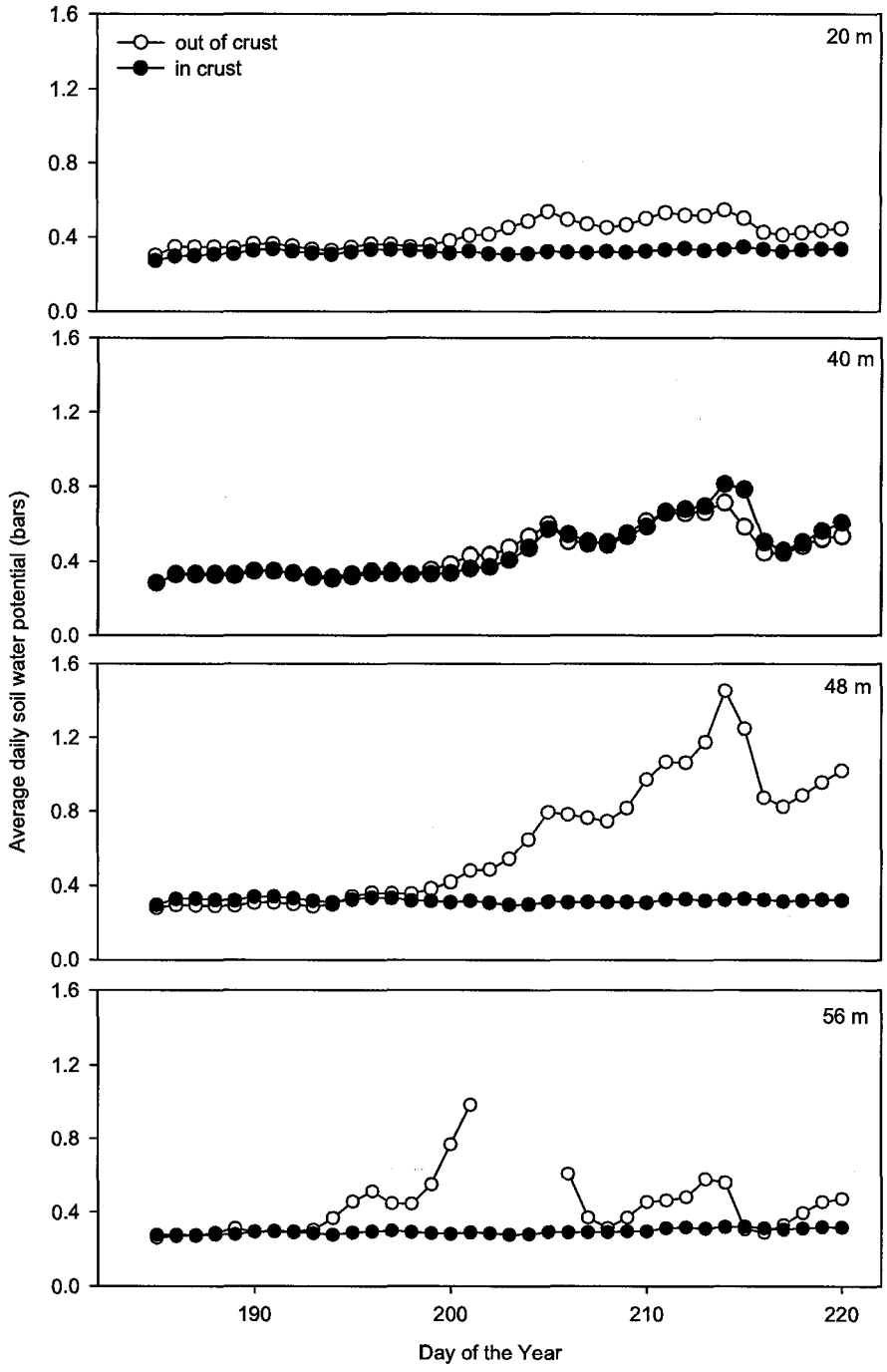

Figure 3.6 Daily mean soil water potential (bars) of crusted and uncrusted surfaces at each of four microclimate sites in front of the Teardrop Glacier, Sverdrup Pass Ellesmere Island, Nunavut from July 3rd to August 7th, 2004. Data are missing for several days in the uncrusted site at 56 m.

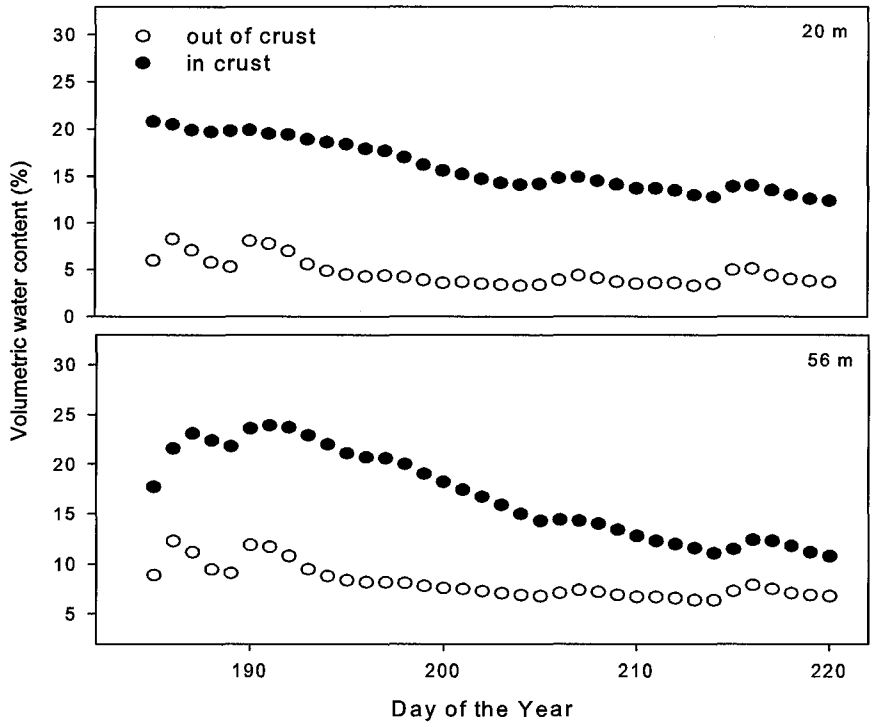

Figure 3.7 Daily mean percent volumetric water content (from TDR) in and out of crust at two microclimate sites in front of the Teardrop Glacier, Sverdrup Pass, Ellesmere Island, Nunavut from July 3rd to August 7th, 2004.

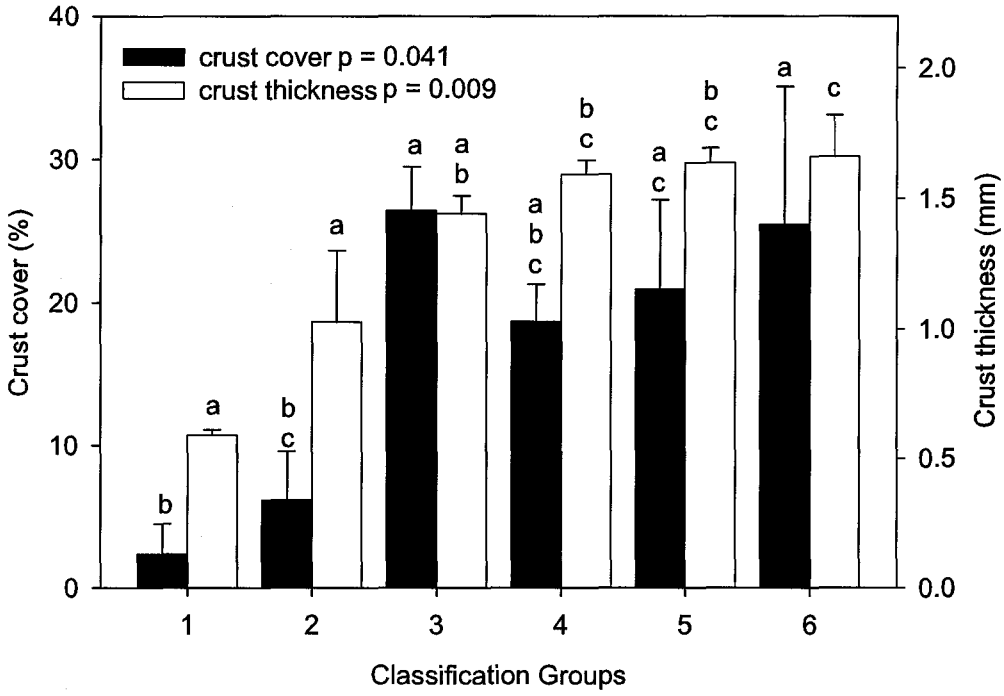

Figure 3.8 Mean crust cover (%) ± SE and thickness (mean ± SE of the 5 thickest crusts) at each classification group with distance from the Teardrop Glacier, Sverdrup Pass, Ellesmere Island, Nunavut. Classification groups are averaged from 20 site values in sequential order: Group 1 (n=2), 2 (n=3), 3 (n=5), 4 (n=3), 5 (n=5), 6 (n=2). Letters denote results of multiple comparison tests following ANOVAs. Groups with the same letters were not significantly different from each other.

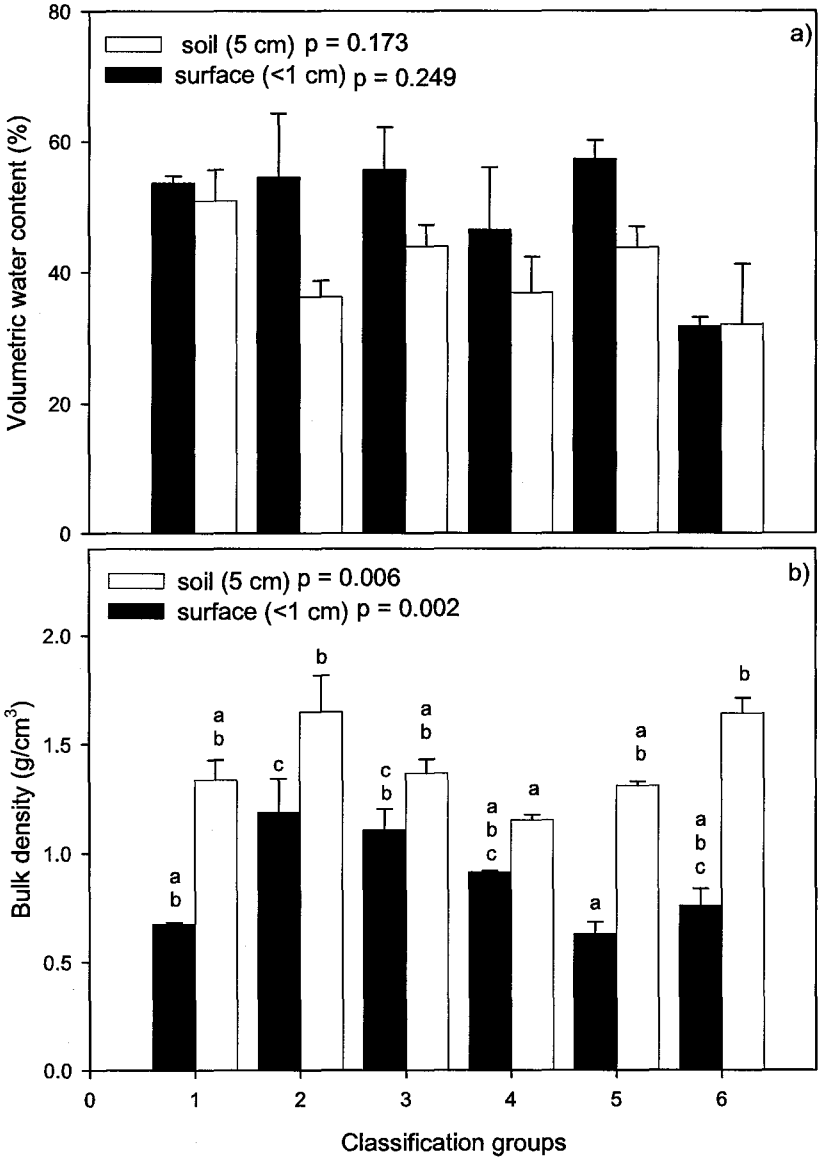

Figure 3.9 a) Volumetric water content and b) bulk density of crusted surface (0.7 cm deep) and soil (5 cm deep) cores at each classification group with distance from the Teardrop Glacier, Sverdrup Pass, Ellesmere Island, Nunavut. Classification Groups are averaged from 20 site values in sequential order: Group 1 (n=2), 2 (n=3), 3 (n=5), 4 (n=3), 5 (n=5), 6 (n=2). Letters denote results of multiple comparison tests following ANOVAs. Groups with the same letters were not significantly different from each other.

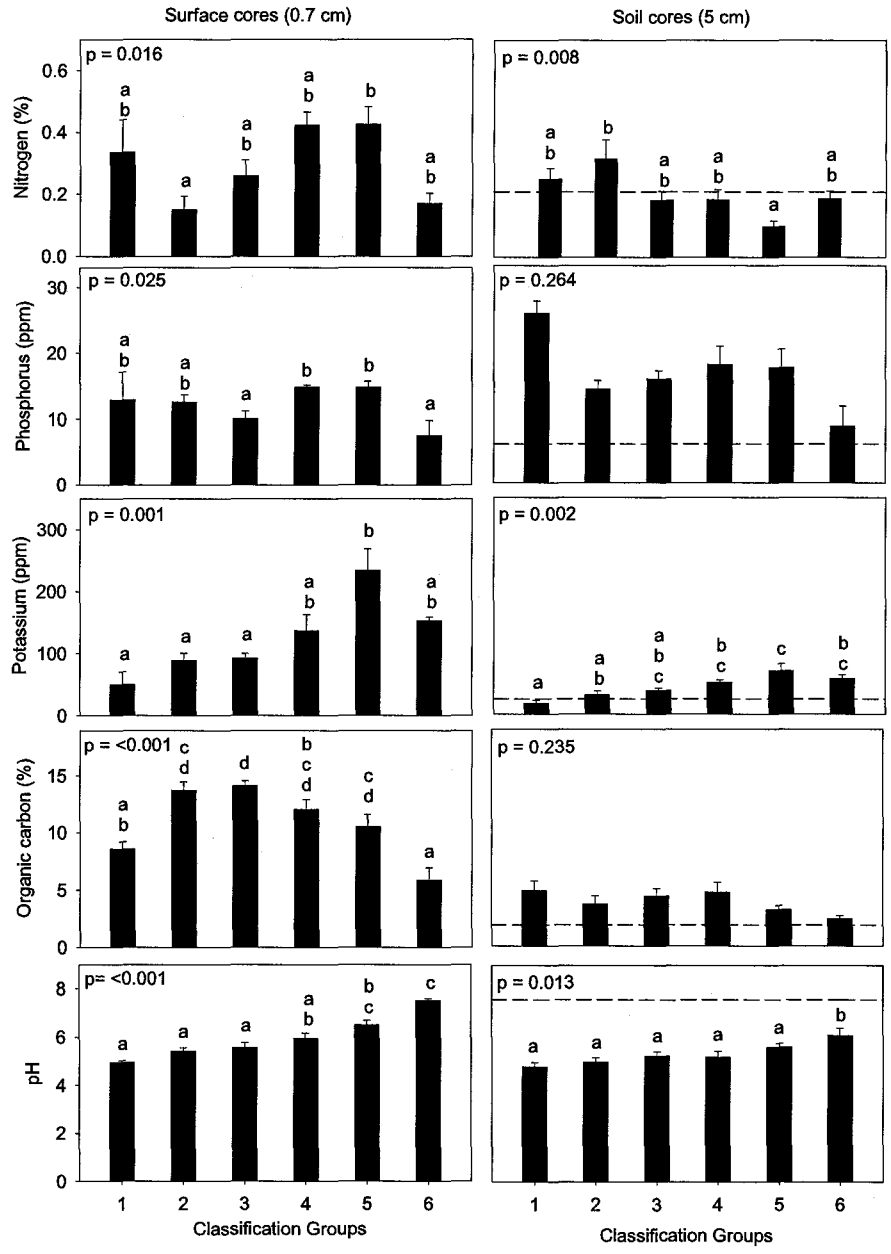

Figure 3.10 Mean nutrient concentrations and pH values of the < 2 mm soil fraction from surface (0.7 cm deep) and soil (5 cm deep) cores at each classification group with distance from the Teardrop Glacier, Sverdrup Pass, Ellesmere Island, Nunavut. The dashed horizontal lines are mean values from Lévesque (1997) and Lévesque *et al* (1997). Classification Groups are averaged from 20 site values in sequential order: Group 1 (n=2), 2 (n=3), 3 (n=5), 4 (n=3), 5 (n=5), 6 (n=2). Letters denote results of multiple comparison tests following ANOVAs. Groups with the same letters were not significantly different from each other.

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ANNEXE 1

SEED RETENTION AND GERMINATION EXPERIMENTS ON BIOLOGICAL SOIL CRUSTS FROM A HIGH ARCTIC GLACIER FORELAND

Through field and laboratory experiments, we tested the hypothesis that soils colonized by biological soil crusts provided a superior substrate for seed retention and germination than soils devoid of crust along a high arctic glacier foreland in Sverdrup Pass, Ellesmere Island, Nunavut (79°10'N, 79°45'W).

METHODS

Seed retention and germination experiments *in situ*

Six experimental 'seed sites' were established with varying distance from the Teardrop Glacier in order to test the ability of crusted and uncrusted substrate to retain seeds and support germination. It was uncommon to find areas of crusted and uncrusted terrain in close proximity to one another, given that soil crusts became the dominant substrate on most of the foreland approximately 20 m from the glacier terminus (< 10 years after retreat; Chapitre 2), accordingly, only isolated patches of uncrusted glacial soil could be found. The experimental sites were situated along the foreland at the following distances; 37 m, 56 m, 69 m, 90 m and 120 m from the glacier with one site beyond the terminal moraine at 208 m. At each of the 6 field sites, 4 crusted and 4 uncrusted round plots were established for each of the germination and retention experiments using an 8.8 cm diameter Petri dish as a template.

Sterilized (autoclaved for 1 hour) sesame seeds (*Sesamum indicum*) were chosen for the retention experiment due to their small size and ability to be seen easily on the surface of most substrates. Lettuce seeds (*Lactuca sativa*) var. "Grand Rapids" and radish, (*Raphanus sativus*) var. "Cherry Bell" were chosen for the germination experiments as they are readily available, small enough to be comparable to arctic seeds and germination trials (at ≤ 10 °C) proved that they would germinate under anticipated arctic summer conditions. Arctic species were not used as these are difficult to find in suitable

quantities and individual life histories would have introduced ecological complications to the experiment. Thirty seeds were scattered randomly over each plot to mimic wind dispersal and plots were monitored every 2 days for 6 weeks for both retention (sesame) and germination (lettuce and radish). Due to the fact that the seed retention and germination experiments were started after spring melt, on July 2, 15 ml of local glacier water was added to each plot in order to reproduce the increased moisture provided by spring snowmelt that would have initiated seed germination earlier in the season.

Laboratory germination experiments

To complement the field germination experiments, a controlled laboratory experiment was performed using crust sampled from varying distances along the foreland. On August 9, 2004 four samples of crust were collected from the vegetation and soil sampling sites described in Chapter 2. Samples of crust were not collected from the first two sites, at 0 and 6 m from the glacier, because crust cover was negligible, therefore crusts were collected from a total of 18 sites. The top 1 cm of substrate, including the crust, was collected using an 8.8 cm diameter Petri dish as a core, the contents sealed with Parafilm, labelled crust side up and shipped frozen at –10 °C. The samples were kept frozen for 3.5 months to simulate a winter dormancy period. Representative examples of uncrusted substrate were not brought back due to the fact that these were rare and consisted of primarily inorganic glacial soil (largely sand) and cost and logistics prevented their shipment. The laboratory germination experiments therefore test the difference between crusts at various distances along the foreland against a control of sterilized sand (autoclaved wet for 1 hour).

In the fall of 2004, 200 ml of sterilised sand was placed in a plastic mini-greenhouse container with lid (height 8 cm, length and width 14 cm: 1568 cm^3; Figure A1.1) to a depth of 1.5 cm. The frozen 1 cm thick crust cores were removed from the Petri dishes November 29, 2004 and placed right side up on top of the sand. The crusts were allowed to come to room temperature before being watered to saturation with deionized water. Fifteen lettuce seeds (*Lactuca sativa* var. Grand Rapids) were spread evenly over each crust surface and the lid on each sample was closed. The containers were then placed in

a growth chamber under 'ideal' summer arctic conditions of 24 hours sunlight and 20 °C (actual average temperature during the experiment 20.9 °C ± 0.4 SE) and rotated every 2 - 3 days. Humidity was kept at 23.3 % ± 3.2 SE and light levels between 700 - 800 μmol/m^2/sec. Crust surfaces were kept moist to saturation and germination was monitored every 2 - 3 days over the course of the 23 day experiment.

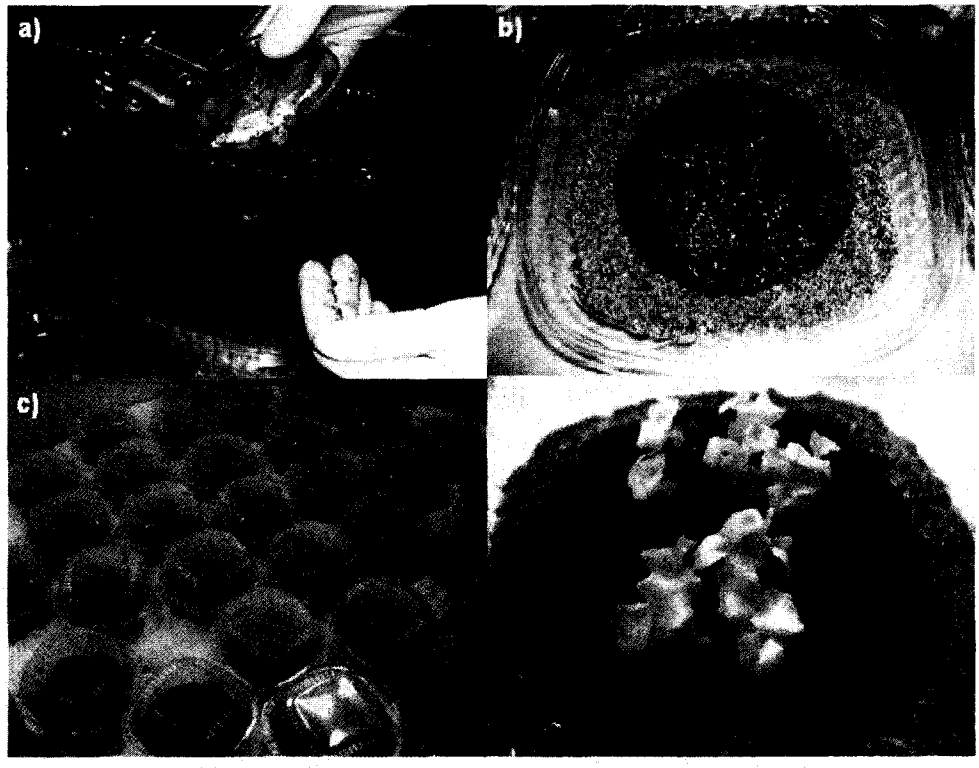

Figure A1.1 Laboratory germination experiments from crusts collected in front of the Teardrop Glacier, Sverdrup Pass, Ellesmere Island, Nunavut. a) frozen crust core placed on sterilized sand; b) crust core seeded with lettuce; c) mini greenhouses within the growth chamber; d) young lettuce plants growing on crust.

After 23 days of growth, the lettuce plants were physically extracted from their growing substrate using de-ionized water. Above and below-ground plant material was separated, washed of all dirt and weighed fresh (precision 0.1 mg). Samples were oven dried at 30 °C for 2 weeks and left in a desiccator for 1 week and reweighed dry. Samples were sent to Université Laval Forestry Soils Lab, Québec City, Canada for analysis of the percentage of total nitrogen in above and below ground plant tissue using the total

Kjeldahl method by flow injection analysis (Parkinson and Allen, 1975). Data obtained at the end of the germination experiment included percent germination success, mean number of lettuce leaves per plant and the nitrogen content of above and below ground lettuce plants.

Analyses

Analyses of variance (one or two-way ANOVAs) were applied to determine significant differences between plants grown on different substrates (crust or control) as well as between sites (distance from the glacier). Whenever data did not meet the assumptions of normality or equal variance, an equivalent non-parametric test was employed. For the field experiments, two-way ANOVAs were used in order to determine whether there were significant differences in seed retention and in germination on crusted and uncrusted substrate and with distance from the glacier at the six seed sites. For the laboratory experiments, the six site classification groups determined in Chapter 2 were used as a proxy for distance to determine whether there were significant differences in the germination success, the number of leaves produced per lettuce plant and the % N in above and below ground lettuce grown on crusts extracted from the sites along the foreland as well as between crust and the control.

RESULTS

Seed retention and germination *in situ*

The percent retention of seeds at each of the experimental crusted and uncrusted field sites yielded very few comparative results as only a limited number of seeds were retained on the surface of either substrate and results varied widely within and among sites. Seed retention in the crusted sites ranged from 0.3 % ± 0.3 SE to 19.4 % ± 5.6 SE and was lower than the retention in the uncrusted sites, which ranged from 0.6 % ± 0.6 SE to 26.9 % ± 4.5 SE. A two-way ANOVA found that there was no significant difference in seed retention between the two substrates or with distance from the glacier. Germination success was also very low at all sites and varied between 0 - 0.83 % in the crusted sites and 0 - 1.7 % on the uncrusted sites. A Kruskal-Wallis one-way ANOVA

on ranks found that there was no significant difference between germination rates on crusted and uncrusted substrates.

Laboratory germination experiments

The germination success, number of leaves and % N in above and below ground lettuce plant tissues were all generally higher when grown in crusts from the foreland than in the control (Figure A1.2). There was no significant difference in the germination success or % N in tissues of lettuce plants growing on crusts across classification groups or between crust and the control, however the mean number of leaves produced per lettuce plant varied significantly across classification groups and was significantly higher in plants grown on crust than on the control (Table A1.1).

Table A1.1 Results of significance tests of germination success, mean number of leaves per plant and nitrogen content in above and below ground plant tissues of *Lactuca sativa* grown on controls of sterilized sand and crusts collected at varying distances from the Teardrop Glacier, Sverdrup Pass, Ellesmere Island, Nunavut. Significant results of one-way ANOVA's ($p < 0.05$) are in bold.

Laboratory experiment	Across classification groups	Crust vs. Control
Germination success (%)	0.318	0.075
Mean number of leaves per plant	**<0.001**	**<0.001**
Nitrogen % above ground	0.063	-
Nitrogen % below ground	0.099	-

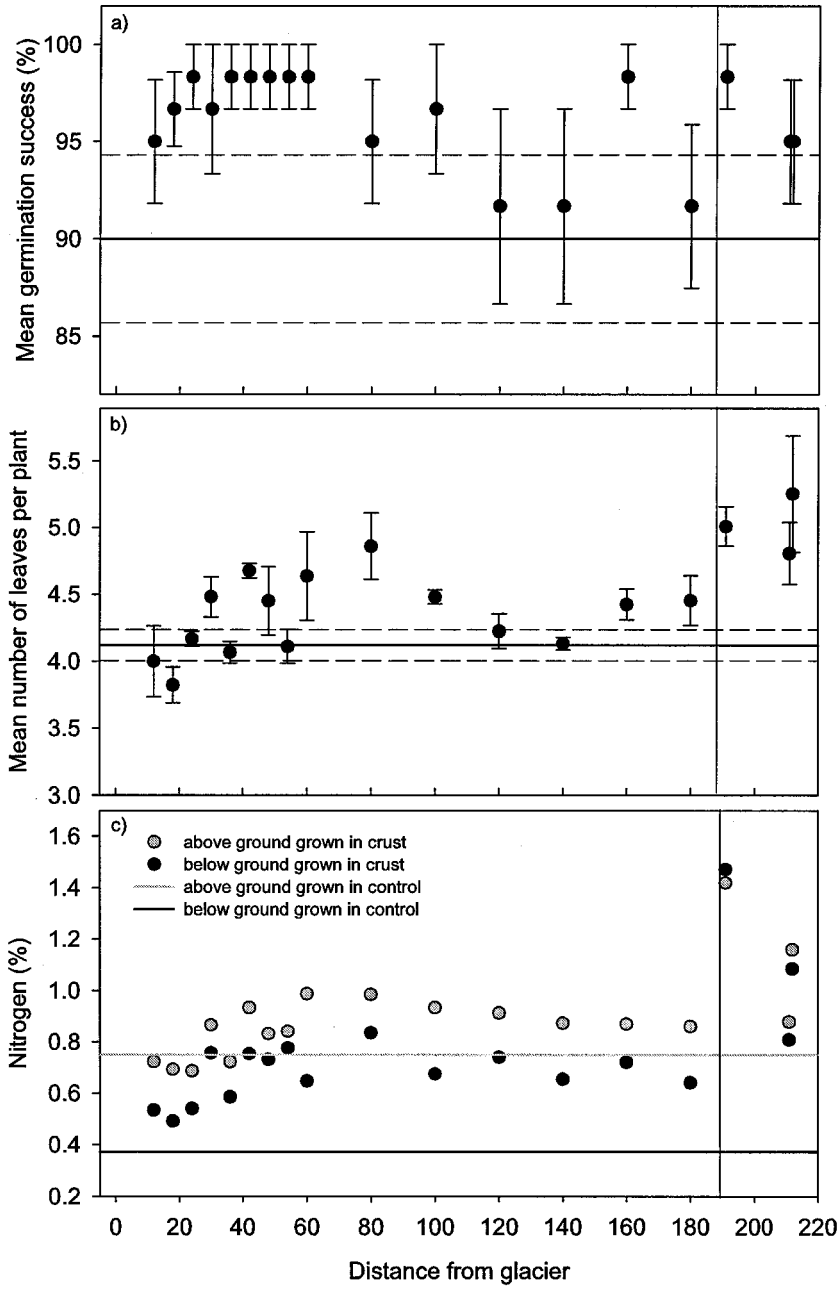

Figure A1.2 Results of germination experiments using seeds of *Lactuca sativa* grown for 23 days at 20 °C, 24 hours sunlight on controls of sterilized sand and crusts collected at varying distances from the Teardrop Glacier, Sverdrup Pass, Ellesmere Island, Nunavut. Dark circles in a) and b) represent means (± SE) of plants grown on crust, horizontal lines indicate mean and SE (solid and dashed lines respectively) of plants grown on controls of sterilized sand. The solid vertical line indicates the position of the terminal moraine at 190 m.

DISCUSSION

Seed retention and germination *in situ*

The low retention observed in the field experiments illustrates the tendency of seeds to move once deposited on the ground. Once seeds moved from the experimental plots they could not be located in the immediate vicinity. Seeds likely moved into soil cracks or were displaced further by wind or water. The presence of a biological soil crust did not appear to improve seed retention or subsequent germination, at least for the short period of time in which our experiments took place. Germination occurred primarily in the holes left by markers defining the small experimental plots, suggesting that seed burial is important. Although a wide variety of seed sizes and shapes exist in the Arctic, it is possible that the size and shape of the seeds used in the experiments may not have accurately reflected retention or germination ability of arctic seeds. Further experimentation in the field with additional seeds and in areas sheltered from the effects of wind or water might elucidate the difference in retention and germination of substrates. It may also be advisable to soak seeds prior to dispersal on the plots since desiccation is a probable source of mortality.

Laboratory germination experiments

The laboratory experiments do not provide robust, statistically significant results but do suggest trends occurring with distance from the glacier. The same general trend of a rapid increase (in germination success, number of leaves and nitrogen content) was also observed in many other characteristics *in situ* such as crust cover and thickness. The higher germination success and the significantly greater number of leaves produced by lettuce plants grown on crusts vs. control suggest that crusts may facilitate germination and growth, perhaps through additional moisture or nutrient availability. Further experimentation is warranted to confirm these trends. Additional investigations of the textural, chemical and biological properties of crusts would improve our understanding of their potential as plant substrates.

ANNEXE 2

TEARDROP GLACIER RETREAT

Retreat rates of glaciers in the High Arctic have been determined by various means including satellite and air photo interpretation as well as direct measurements of retreat *in situ*. The first and only detailed aerial photographic survey of the Queen Elizabeth Islands occurred in 1959. Comparisons between the 1959 air photographs, in combination with direct *in situ* measurements, allowed Fahselt *et al.* (1988) to determine that the mean annual retreat rate of the Teardrop Glacier between 1959 and 1986 was 1.6 m/yr ± 0.1 SE. Researchers working in Sverdrup Pass during the late 1980's and early 1990's, including Fahselt *et al.* (1988), established a network of stakes marking the position of the glacier terminus. Ten references stakes were established on June 28th, 1987 and placed 10 m from the ice edge. On July 26, 1992 another set of stakes was placed in line with the 1987 stakes 5 m from the ice edge (Josef Svoboda, University of Toronto, pers.com).

During the 2004 field season, some of the stakes from this original network were found, permitting the calculation of glacier retreat since 1987 and 1992. Table A2.1 shows the estimated retreat rates for various time periods between 1959 and 2004. Jones (1997) visited this foreland in July 1995 and noted that the glacier was 170 m from the terminal moraine. Given that the foreland was 190 m long as of June 2004 a retreat rate of 2.2 m/year was calculated based on 20 m of retreat in 9 years. During the 2004 summer field season alone, the ice margin was found to have retreated 3.35 m ± 0.05 SE (n = 2 markers) in a period of 41 days from June 29th and August 9th however it is not clear whether this measurement was taken from the true ice margin or a snow flush line. Year to year measurements allow for greater accuracy of measurement and avoid such errors.

To estimate yearly retreat rate we had to assume that the retreat rate of the Teardrop Glacier remained constant during each time interval. Some of the variability in retreat rates can be attributed to the different methods of measurement used by different researchers (topometers, tape measurers, GPS, air photos) as well as the time of year that

stakes were established and measured. For example, the 1987 and 1992 reference stakes were set out at different times of year (June 28th and July 26th respectively). As can be seen from the rapid summer melt witnessed in 2004, the difference of a few weeks can alter the estimates of overall retreat. Despite this coarse approach, our data show that melting has obviously increased since initial retreat rates were first determined by Fahselt *et al.* (1988).

On August 9th, 2004, twelve new reference stakes marking the position of the glacier were added to the existing network of stakes in order to allow for future long term monitoring of the Teardrop Glacier's retreat.

Table A1.1 Mean annual retreat of the Teardrop Glacier, Sverdrup Pass, Ellesmere Island, Nunavut (79°10'N, 79°45'W).

Years	Sample size	Mean retreat rate (m/yr)(± SE)	Notes
1959 - 1986	9	1.6 ± 0.11	Fahselt *et al.*1988
1987 - 1992	1	1.88	*in situ* from existing glacier markers
1987 - 2004	2	1.61 ± 0.19	*in situ* from existing glacier markers
1992 - 2004	7	2.01± 0.13	*in situ* from existing glacier markers
1995 - 2004	1	2.22	Jones (1997)
2004 summer	2	3.35 ± 0.05 m	*in situ* from glacier markers

ANNEXE 3

MEASUREMENTS OF THE LICHEN, *XANTHORIA ELEGANS* AND THE RUSH, *LUZULA CONFUSA*

Terrain age estimates on glacier forelands are often determined using plants that display known yearly growth increments such as *Salix* sp. (Jones, 1997), *Cassiope tetragona* (L.) D. Don subsp. *tetragona* (Rayback and Henry, 2005) or clump diameters of species with known growth rate curves (Whittaker, 1993). Lichenometry can also be used but is often unsuitable on young terrain such as that released since the Little Ice Age, due to the amount of time required for long-lived saxicolous lichens to become established.

Luzula confusa Lindberg has been deemed a useful alternative to lichenometry on another high arctic foreland (Jones, 1997) due to its rapid colonisation, widespread abundance and environmental tolerance. The radial growth pattern allows *Luzula confusa* clumps to be measured in two orthogonal directions. The average of these two measurements was used to come up with a single plant width. Where possible, the five largest clumps were used to provide a largest mean width value per site. Measurements of the lichen, *Xanthoria elegens* (Link) Th. Fr., growing on rocks were also taken of the five largest widths where available, measured in only one direction.

Measurements were collected in order to determine a relationship between growth and age (Figure A3.1). A regression was plotted between distance from the glacier (proxy for terrain age) in relation to plant size. *Luzula* clump diameters increased logarithmically with distance across the foreland ($r^2 = 0.87$) whereas lichen widths across the foreland grew according to a quadratic equation ($r^2 = 0.98$).

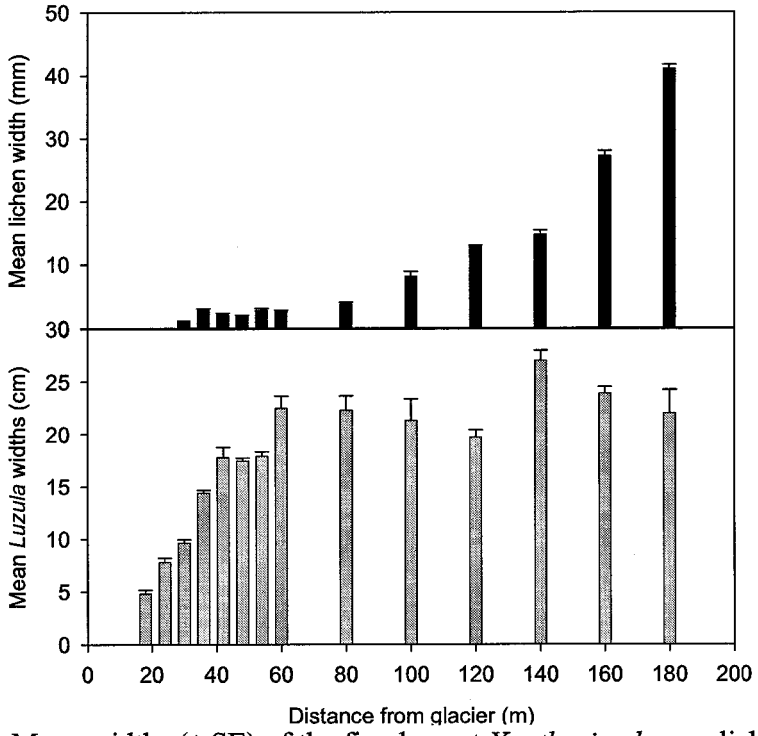

Figure A3.1 Mean widths (± SE) of the five largest *Xanthoria elegens* lichen and *Luzula confusa* across the Teardrop Glacier foreland, Sverdrup Pass, Ellesmere Island, Nunavut.

ANNEXE 4

Table A4.1: Mean vegetation cover and frequency (%) in each of the 20 sites along the Teardrop Glacier and adjacent moraine, Sverdrup Pass, Ellesmere Island, Nunavut. C = % cover, F = % frequency. See Table 2.2 for species authorities.

Distance from glacier (m)	0		6		12		18		24		30		36		42		48	
	C	F	C	F	C	F	C	F	C	F	C	F	C	F	C	F	C	F
Alopecurus borealis	0.01	2.63	0.02	2.17	0.13	4.69	0.11	24.24	1.31	32.56	0.50	50.00	0.54	63.33	0.26	33.33	0.73	60.00
Arctagrostis latifolia																		
Bistorta vivipara																		
Braya glabella									0.01	2.33								
Braya thorild-wulffii									0.01	4.65								
Cardamine bellidifolia									0.01	2.33					0.01	3.33		
Carex aquatilis																		
Carex fuliginosa																		
Carex nardina						1.56							0.01	3.33				
Carex rupestris																		
Cassiope tetragona																		
Cerastium alpinum															0.12	3.33		
Draba cinerea							0.01	3.03	0.05	9.30	0.03	13.33	0.02	6.67	0.03	10.00		
Draba corymbosa									0.01	4.65	0.02	6.67	0.03	13.33	0.06	23.33	0.04	16.67
Draba oblongata			0.00	0.72	0.02	6.25	0.06	24.24	0.13	37.21	0.11	43.33	0.04	10.00	0.04	16.67	0.06	23.33
Draba subcapitata							0.04	15.15	0.03	13.95	0.09	36.67	0.05	20.00	0.05	13.33	0.02	6.67
Draba lactea					0.00	1.56	0.01	3.03	0.03	13.95	0.05	20.00	0.11	36.67	0.07	26.67	0.14	43.33
Dryas integrifolia																		
Eriophorum angustifolium																		
Erysimum pallasii															0.01	3.33		
Eutrema edwardsii																		
Festuca brachyphylla									0.01	2.33	0.01	3.33	0.03	6.67			0.01	3.33
Juncus biglumis											0.02	6.67	0.01	3.33	0.02	6.67	0.03	13.33

Distance from glacier (m)	0		6		12		18		24		30		36		42		48	
	C	F	C	F	C	F	C	F	C	F	C	F	C	F	C	F	C	F
Luzula arctica							0.01	3.03	0.03	6.98	0.08	16.67	0.18	23.33	0.26	40.00	0.45	33.33
Luzula confusa							0.10	33.33	0.43	65.12	1.66	93.33	2.43	96.67	3.16	93.33	3.07	96.67
Minuartia rubella							0.05	18.18	0.02	6.98	0.04	16.67	0.01	3.33	0.01	3.33	0.01	3.33
Oxyria digyna											0.10	6.67	0.06	6.67				
Papaver radicatum			0.01	2.17	0.02	7.81	0.02	9.09	0.08	13.95	0.26	40.00	0.34	40.00	0.49	43.33	0.08	20.00
Pedicularis hirsuta																		
Pleuropogon sabinei																		
Poa abbreviata							0.01	3.03	0.08	13.95	0.03	3.33	0.04	10.00	0.08	13.33	0.14	20.00
Poa arctica					0.02	6.25	0.01	3.03	0.15	11.63	0.26	23.33	0.29	23.33	0.14	6.67	0.01	3.33
Potentilla hyparctica																		
Potentilla nivea															0.01	3.33		
Potentilla pulchella																	0.01	3.33
Puccinellia bruggemannii					0.01	3.13			0.08	16.28	0.13	10.00	0.02	6.67				
Ranunculus sulphureus																		
Salix arctica							0.02	6.06	0.02	4.65	0.34	20.00	0.57	33.33	1.12	30.00	0.88	33.33
Saxifraga cespitosa									0.02	2.33	0.03	3.33	0.13	30.00	0.03	10.00	0.01	3.33
Saxifraga cernua			0.01	1.45	0.01	3.13	0.09	30.30	0.49	83.72	0.38	76.67	0.52	96.67	0.26	80.00	0.24	83.33
Saxifraga foliolosa											0.03	10.00	0.03	13.33	0.09	23.33	0.06	23.33
Saxifraga hirculus																		
Saxifraga nivalis/tenuis					0.00	1.56	0.04	15.15	0.03	11.63	0.12	40.00	0.17	43.33	0.06	23.33	0.08	33.33
Saxifraga oppositofolia					0.03	10.94	0.30	48.48	0.63	76.74	1.43	100	1.43	93.33	1.68	80.00	1.91	80.00
Saxifraga platysepala											0.00	3.33						
Saxifraga rivularis			0.00	1.45	0.00	1.56	0.04	15.15	0.07	23.26	0.18	63.33	0.07	26.67	0.05	20.00	0.03	10.00
Saxifraga tricuspidata									0.03	6.98	0.03	10.00	0.10	10.00	0.05	3.33	0.03	10.00
Silene acaulis																		
Silene uralensis													0.01	3.33				
Stellaria longipes					0.05	1.56	0.07	12.12	0.42	34.88	1.26	53.33	1.99	66.67	1.23	56.67	1.72	86.67

Distance from glacier (m)	54		60		80		100		120		140		160		180	
	C	F	C	F	C	F	C	F	C	F	C	F	C	F	C	F
Alopecurus borealis	1.31	80.00	0.49	58.33	0.23	34.78	0.03	12.50	0.14	38.46	0.03	10.00			0.12	28.00
Arctagrostis latifolia													1.28	25.00		
Bistorta vivipara			0.02	8.33	0.02	8.70			0.08	23.08	0.11	35.00	0.58	70.00	0.43	56.00
Braya glabella																
Braya thorild-wulffii																
Cardamine bellidifolia	0.01	3.33	0.01	4.17	0.01	4.35	0.04	16.67	0.01	3.85	0.06	25.00	0.06	25.00	0.07	28.00
Carex aquatilis					0.03	4.35			4.58	65.38	0.38	5.00	0.76	35.00	0.58	12.00
Carex fuliginosa							0.01	4.17	0.05	11.54	0.09	10.00	0.20	35.00	0.09	16.00
Carex nardina											0.13	15.00				
Carex rupestris							0.00	4.17								
Cassiope tetragona			0.01	4.17	0.01	4.35					0.05	10.00	0.01	5.00	0.30	4.00
Cerastium alpinum	0.03	3.33					0.05	12.50								
Draba cinerea																
Draba corymbosa	0.04	16.67	0.01	4.17			0.09	37.50	0.01	3.85	0.03	10.00	0.06	25.00	0.02	8.00
Draba oblongata	0.02	6.67	0.03	12.50												
Draba subcapitata	0.01	3.33							0.01	3.85					0.01	4.00
Draba lactea	0.13	33.33	0.07	29.17	0.04	17.39	0.13	41.67	0.01	3.85	0.05	20.00	0.04	15.00	0.05	12.00
Dryas integrifolia			0.19	12.50	0.39	21.74	0.33	29.17	0.35	46.15	2.09	65.00	1.84	45.00	0.58	28.00
Eriophorum angustifolium					0.03	4.35			0.35	26.92	0.08	5.00	0.35	25.00	0.12	20.00
Erysimum pallasii																
Eutrema edwardsii													0.01	5.00		
Festuca brachyphylla	0.10	16.67			0.01	4.35									0.05	12.00
Juncus biglumis	0.04	16.67	0.01	4.17	0.03	13.04			0.06	23.08	0.01	5.00	0.05	20.00	0.04	8.00

Distance from glacier (m)	54		60		80		100		120		140		160		180	
	C	F	C	F	C	F	C	F	C	F	C	F	C	F	C	F
Luzula arctica	0.75	56.67	0.21	54.17	0.43	69.57	0.55	87.50	0.26	57.69	0.38	65.00	0.80	65.00	0.32	56.00
Luzula confusa	3.95	100.00	5.23	91.67	7.45	100.00	5.74	100.00	3.07	84.62	3.81	90.00	5.20	80.00	2.01	88.00
Minuartia rubella			0.01	4.17	0.03	13.04	0.02	8.33			0.01	5.00	0.01	5.00		
Oxyria digyna					0.01	4.35	0.03	4.17							0.02	8.00
Papaver radicatum	0.05	20.00	0.14	25.00	0.10	21.74	0.15	29.17	0.02	7.69	0.08	20.00	0.11	20.00	0.06	16.00
Pedicularis hirsuta					0.35	39.13	0.51	66.67	0.42	61.54	0.51	75.00	0.18	35.00	0.24	52.00
Pleuropogon sabinei									0.13	3.85			0.18	5.00		
Poa abbreviata	0.03	3.33	0.01	4.17							0.03	10.00	0.04	5.00	0.06	4.00
Poa arctica	0.08	6.67			0.10	21.74	0.06	16.67	0.09	15.38	0.24	30.00	0.23	25.00	0.09	16.00
Potentilla hyparctica					0.01	4.35					0.01	5.00	0.09	25.00	0.19	40.00
Potentilla nivea									0.03	11.54	0.03	10.00	0.03	10.00	0.01	4.00
Potentilla pulchella			0.01	4.17												
Puccinellia bruggemannii																
Ranunculus sulphureus																
Salix arctica	0.28	26.67	4.56	83.33	9.98	91.30	8.75	100.00	6.35	84.62	10.33	95.00	6.04	85.00	10.17	84.00
Saxifraga cespitosa	0.01	3.33	0.03	4.17	0.01	4.35	0.07	8.33								
Saxifraga cernua	0.26	80.00	0.23	70.83	0.08	30.43	0.06	25.00	0.04	15.38	0.01	5.00	0.06	25.00	0.01	4.00
Saxifraga foliolosa	0.13	43.33	0.04	16.67	0.08	30.43	0.02	8.33	0.05	19.23	0.04	15.00	0.08	30.00	0.03	12.00
Saxifraga hirculus													0.01	5.00		
Saxifraga nivalis/tenuis	0.04	16.67	0.08	29.17	0.05	21.74	0.02	8.33	0.02	7.69	0.01	5.00	0.05	20.00	0.02	8.00
Saxifraga oppositofolia	0.72	36.67	2.25	79.17	2.89	82.61	2.23	87.50	2.02	65.38	2.91	90.00	1.24	75.00	1.03	68.00
Saxifraga platysepala																
Saxifraga rivularis	0.06	23.33	0.01	4.17												
Saxifraga tricuspidata			0.67	33.33	0.08	13.04	0.01	4.17	0.07	11.54	0.73	40.00			0.03	4.00
Silene acaulis							0.00	4.17								
Silene uralensis	0.01	3.33	0.02	8.33			0.08	33.33			0.05	10.00	0.03	10.00	0.02	8.00
Stellaria longipes	0.88	70.00	0.73	62.50	1.18	60.87	0.40	70.83	0.31	42.31	0.21	50.00	0.28	55.00	0.11	44.00

Distance from glacier (m)	191		211		212	
	C	F	C	F	C	F
Alopecurus borealis	0.01	4.55	0.13	6.67	0.05	19.05
Arctagrostis latifolia	0.18	18.18	0.03	3.33	0.11	42.86
Bistorta vivipara	0.88	72.73	0.03	6.67	1.62	80.95
Braya glabella						
Braya thorild-wulffii						
Cardamine bellidifolia	0.03	13.64			0.01	4.76
Carex aquatilis	0.56	22.73	0.02	6.67	3.00	76.19
Carex fuliginosa	0.88	77.27	0.18	10.00	0.17	33.33
Carex nardina	0.01	4.55				
Carex rupestris						
Cassiope tetragona	0.38	9.09				
Cerastium alpinum						
Draba cinerea			0.02	6.67		
Draba corymbosa	0.01	4.55	0.03	10.00	0.02	9.52
Draba oblongata			0.06	23.33		
Draba subcapitata			0.02	6.67		
Draba lactea	0.08	31.82	0.01	3.33	0.12	47.62
Dryas integrifolia	4.25	59.09	1.13	20.00	0.51	19.05
Eriophorum angustifolium	2.03	59.09	0.76	13.33	0.33	38.10
Erysimum pallasii					0.17	4.76
Eutrema edwardsii					0.02	9.52
Festuca brachyphylla	0.02	9.09			0.35	28.57
Juncus biglumis	0.24	86.36			0.15	61.90

Distance from glacier (m)	191		211		212	
	C	F	C	F	C	F
Luzula arctica	0.25	68.18	0.02	6.67	0.21	57.14
Luzula confusa	0.11	22.73			0.20	19.05
Minuartia rubella	0.03	13.64			0.10	38.10
Oxyria digyna	0.13	40.91	0.01	3.33	0.19	14.29
Papaver radicatum	0.05	18.18			0.06	23.81
Pedicularis hirsuta	0.15	50	0.22	23.33	0.26	47.62
Pleuropogon sabinei						
Poa abbreviata			0.13	23.33	0.04	4.76
Poa arctica	0.23	13.64	0.08	6.67	0.18	9.52
Potentilla hyparctica	0.14	45.45			0.15	42.86
Potentilla nivea			0.09	13.33		
Potentilla pulchella			0.08	16.67	0.01	4.76
Puccinellia bruggemannii						
Ranunculus sulphureus					0.02	9.52
Salix arctica	5.77	100	7.82	76.67	13.14	95.24
Saxifraga cespitosa						
Saxifraga cernua	0.05	18.18	0.01	3.33	0.12	23.81
Saxifraga foliolosa	0.08	31.82				
Saxifraga hirculus						
Saxifraga nivalis/tenuis	0.01	4.55			0.01	4.76
Saxifraga oppositofolia	3.26	77.27	0.73	73.33	2.60	90.48
Saxifraga platysepala						
Saxifraga rivularis						
Saxifraga tricuspidata						
Silene acaulis						
Silene uralensis	0.07	27.27	0.01	3.33	0.12	47.62
Stellaria longipes	0.15	40.91	0.02	6.67	0.21	66.67